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Phylogeny and origin of Jurassic irregular echinoids (Echinodermata: Echinoidea)

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Abstract – A phylogenetic analysis of Jurassic irregular echinoids is realized to explore the origin and early evolution of this important subset of echinoids. The phylogeny is based on 39 characters and considers data from apical system architecture, the corona including tuberculation and spines, Aristotle's lantern, and general test shape. Results corroborate the monophyly of Irregularia, and clarify the phylogenetic interrelationships existing between the main groups of irregular echinoids. Specializations of the Aristotle's lantern, spines, tubercles and phyllodes constitute the apomorphies for different taxa, as for the whole of Irregularia. The phylogenetic signal yielded by these characters highlights the importance of the environmental context of the origin and diversification of irregular echinoids. The definition of 'irregularity' is re-examined, rejecting exocyclism and characters of the apical system as appropriate synapomorphies, and stressing the importance of other characters, particularly the high density and small size of tubercles and spines. A new clade name, Infraclypeidae [P], and phylocode designations (stem-based diagnoses) are proposed for the clades Irregularia, Eognathostomata, Microstomata, Neognathostomata and Atelostomata. Other groupings formerly used (Pygasteroida, Galeropygidae and Menopygidae) are considered paraphyletic.

Keywords: Irregularia, Echinoidea, phylogeny, systematics, Jurassic.

1. Introduction

1.a. Irregular echinoids

The mass extinction that took place at the end of the Permian deeply affected echinoid diversity. Only two lineages survived the event (Kier, 1965, 1968, 1974, 1977, 1984; Fell, 1966; Smith, 1984; Smith & Hollingworth, 1990). Once past the 'Palaeozoic' crisis, echinoid diversity recovered through significant evolutionary radiation and rapid morphological diversification (Kier, 1974, 1982; Smith, 1978*b*, 1984). The echinoids therefore played a much more prominent role in Mesozoic echinoderm diversity than they did previously (Erwin, 1993). Diversity increased from the Early Jurassic (Sprinkle, 1983) with the appearance of a large and important group of echinoids: the irregular sea urchins, recognized as the clade Irregularia Latreille, 1825 (Kier, 1977, 1982; Smith, 1984, 1988). This clade includes forms as diverse as the present-day lamp urchins, heart urchins and sand dollars, and constitutes nearly 60 % of extant and extinct species of echinoids (calculated after Kier, 1974). The appearance of irregular sea urchins thus contributes greatly to the general recovery and expansion of echinoid diversity that occurs within the global context of the 'Mesozoic Marine Revolution' (MacLeod, 2003; Vermeij, 1977, 1995).

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The establishment of an anterior–posterior axis of secondary bilateral symmetry in the otherwise pentaradial tests of the Irregularia distinguishes them from the other globose sea urchins (sometimes referred to as 'regular' urchins), and places the radiation of irregular sea urchins among the most significant events in the evolution of echinoids. The establishment of secondary bilateral symmetry is associated with the migration of the periproct (the area which surrounds the anus) from the summit of the test toward the posterior margin. This migration accompanies other morphological innovations such as the anteriorly placed mouth, the single-direction locomotory systems with spines specialized to produce an efficient power-stroke, the sophisticated particle-picking mechanism that provides continuous access to fresh and abundant supplies of food, and the miniaturization of almost all external appendages such as spines and podia. All these morphological innovations are strongly linked with the colonization and the adaptation to new ecological niches, determined by the nature of the sea bottom where irregular sea urchins live. Irregular echinoids are exclusively microphagous species that can only ingest small nutrient-bearing particles (De Ridder & Lawrence, 1982). This feeding behaviour implies a specialization of the body form and appendages for feeding and moving upon or inside soft sediments (Kier, 1974; Smith, 1981; Kanazawa, 1992; Telford & Mooi, 1996).

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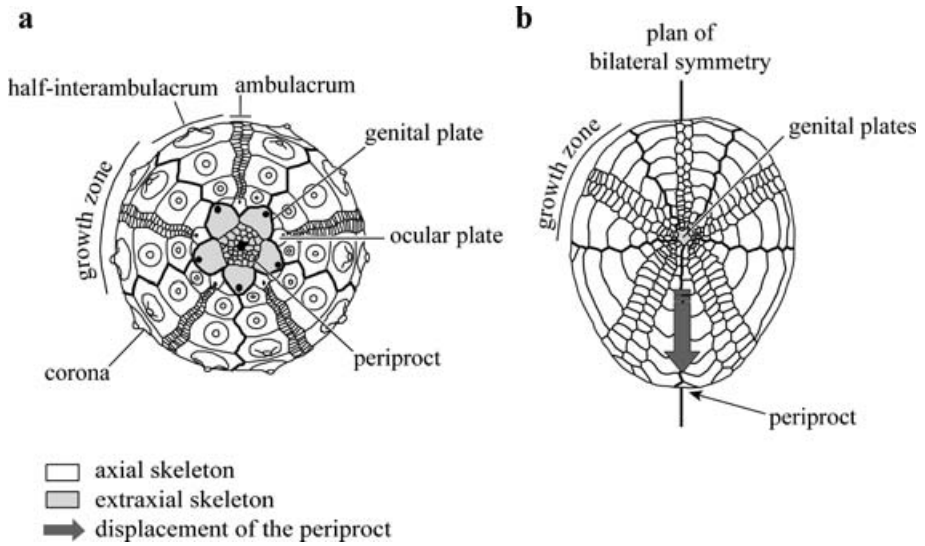


Figure 1. According to the Extraxial–Axial Theory, the echinoid test is constructed almost entirely from axial elements organized into five growth zones. In regular echinoids, the periproct is enclosed within the apical system, a composite structure that gathers ocular (axial elements) and genital (extraxial elements) plates that surround the periproct (extraxial elements) (a, from David & Mooi, 1999). Conversely, in irregular echinoids, the migration of the periproct leads to a breaking of the extraxial region into two distinct units: the genital plates that stay in an apical position, and the periproct that move towards the margin of the test (b).

David & Mooi (1996) have proposed a new system for interpretation of the body wall components among echinoderms (David & Mooi, 1998, 1999; David, Mooi & Telford, 1995; Mooi & David, 1997, 1998). This new system (the Extraxial-Axial Theory, or EAT) bases the recognition of homologies on the embryology and the ontogeny of structures (David & Mooi, 1996, 1998; Mooi, David & Marchand, 1994). It identifies two major body wall categories in the Echinodermata: axial and extraxial. The identification of these two distinct body wall regions permitted the establishment of new homologies pertaining to all echinoderms. In some cases, it also led inexorably to drastic challenges of previous phylogenetic hypotheses (David & Mooi, 2000; Mooi & David, 1998).

Echinoids are unique among the echinoderms because the entire coronal part of the test consists of axial body wall (Mooi, David & Marchand, 1994). The extraxial region is restricted and indeed constricted to the scales present on the periproctal membrane and to the genital plates (Fig. 1). The axial region of the corona is organized into five growth zones that form and continue to grow in accordance with the 'Ocular Plate Rule' (OPR). Following this mechanism, each growth zone is closely associated with an ocular plate and consists of an ambulacrum surrounded by two half-interambulacra, one on each side of the ambulacrum. New ambulacral and interambulacral plates are formed next to the ocular plate. Plates are shifted away from the apical system and the ocular plate as new plates are added at the edge of the oculars between the oculars and the rest of the plate column.

The apical system is a composite structure that associates ocular (axial element) and genital (extraxial element) plates that surround the periproct (extraxial) in 'regular' echinoids (Fig. 1a). In irregular echinoids, the migration of the periproct leads to a 'breaking' of the apical system as the periproct moves out of the circle formed by the genital and ocular plates. This phenomenon is called exocyclism. Exocyclism entails a disruption of the echinoid's small remaining extraxial region into two distinct units: (1) genital plates that remain in the apical position; (2) the periproct and its associated scales that move toward the margin (and in some cases all the way to the oral surface) of the test (Fig. 1b). Therefore, the diversification of irregular echinoids is associated with exocyclism that corresponds to a disruption of the extraxial part of the body into two separate areas.

1.b. Previous works and systematics

According to Melville & Durham (1966), irregular echinoids constitute a morphological (and not taxonomic) group or grade that can be distinguished from 'regular' forms by the position of the periproct outside the apical system (exocyclism), by the predominance of bilateral symmetry in test outlines, and by the absence of the Aristotle's lantern in many of them. Variation in expression of test outline and the Aristotle's lantern implies that these characters cannot constitute absolute criteria for establishment of a natural group of irregular echinoids. In addition, Durham & Wagner (1966) use the terms 'irregular' and 'exocyclic' as synonyms. These terms refer to tests with the periproct located outside the apical system and supposedly contrast with 'regular' and 'endocyclic' which refer to tests with the periproct located within the apical system. Finally,

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irregular, or exocyclic, groupings are recognized to be polyphyletic, the subclass rank of the group is abandoned, and 'irregular echinoid' is retained only as an informal division (Melville & Durham, 1966).

At the same time, Jesionek-Szymanska (1959) and Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) showed that the boundary between regularity and irregularity is not so definite. The morphological changes from the regular to the irregular condition occurred in stages, so that many Jurassic irregular echinoids display intermediate morphologies between regularity and fully manifested irregularity (Jesionek-Szymanska, 1963; Mintz, 1968). Therefore, according to these authors, some Jurassic irregular echinoids are still endocyclic (the periproct is located within the apical system), and exocyclism and irregularity are not good synonyms. If we consider restriction of the concept of irregularity (exocyclism in which the periproct moves significantly away from the centre of the apical system so that it eventually loses contact with it) to the clade that we now consider the Irregularia, we are still left with evidence suggesting that some form of exocyclism (that is, at least some movement of the periproct away from the center of the apical system in the direction of interambulacrum 5) occurred at least seven times in independent lineages of 'regular' echinoids (Saucède, Mooi & David, 2003). Consequently, exocyclism is not a sufficient criterion to define irregularity. Repeated movements of the periproct toward and into interambulacrum 5 could be seen as supporting the plural origin of irregular echinoids, as suggested by Melville & Durham (1966).

As a morphological character of irregular echinoids, exocyclism was given great taxonomic weight in the 19th and the beginning of the 20th century, but the question of the origin of the group, whether unique or plural, was not necessarily tackled. Some authors considered exocyclism to be of major taxonomic importance and placed irregular echinoids in a unique category (Desor, 1855–1858; Wright, 1855–1860; Zittel, 1876–1880; Gregory, 1900). For others, the presence or absence of the Aristotle's lantern was of paramount importance, and echinoids were divided accordingly into those that lack a lantern (the atelostomes) and those that possess one (the gnathostomes). Even in cases when irregular echinoids were recognized, they were split within two distinct groups according to the presence or absence of the Aristotle's lantern (Pomel, 1869, 1883; Lambert & Thiéry, 1909–1925). Finally, certain authors (e.g. Duncan, 1889) did not make a distinction between regular and irregular forms, and species that we now recognize as irregular taxa were scattered among widely disparate groups.

The position favouring the plural origin of irregular echinoids prevailed for most authors of the 20th century. Hawkins (1922) was the first to tackle the question of the origin of irregular echinoids. He derived them from 'regular' echinoids through two independent lineages and two possible ancestors: (1) the Microstomata (*sensu* Smith, 1984) through the genus *Pseudopygaster* Hawkins, 1922 (= *Loriolella* Fucini, 1904) on the one hand, and (2) the Eognathostomata (*sensu* Smith, 1981) through the genus *Plesiechinus* Pomel, 1883 on the other hand.

Mortensen (1948) proposed independent origins for the two families composing the Eognathostomata: the Pygasteridae Lambert, 1899 and the Holectypidae Lambert, 1899. His assumption relied on the absence of tubercle crenulation in certain species of Pygasteridae (as in the 'regular' Pedinidae Pomel, 1883), contrasting this condition with the crenulate tubercles of Holectypidae (as in the 'regular' Diadematidae Gray, 1855). However, he maintained both families, Holectypidae and Pygasteridae, in the same order, and all irregular echinoids in a unique subclass. Later, Jesionek-Szymanska (1970) and Rose & Olver (1984) showed that Pygasteridae have primitive crenulate tubercles, and that crenulation tends to disappear in derived species of *Pygaster* Agassiz, 1836.

In spite of this, the hypothesis of irregular polyphyly has especially been supported by studies of the Aristotle's lantern. These studies followed initial work by Jackson (1912), and the first observations on the Aristotle's lantern and associated structures in irregular echinoids were published on the Eognathostomata (Hawkins, 1934). Durham & Melville (1957) used lantern and tooth morphology to derive irregular echinoids from aulodont and stirodont regular ancestors through three distinct lineages: (1) the Pygasteroida Durham & Melville, 1957, (2) the Gnathostomata Zittel, 1879 (holectypoids and clypeasteroids) and (3) the Atelostomata Zittel, 1879. They concluded that the group Irregularia is polyphyletic and should be abandoned, a position which prevailed in the widely followed *Treatise on Invertebrate Palaeontology* (Durham, 1966). The independence of pygasteroids and holectypoids was also supported by Melville's work (1961) on tooth shape. He compared the apparent triangular shape of teeth in the genus *Pygaster* (pygasteroid) to the keeled teeth of the genus *Holectypus* Desor, 1842 (holectypoid). Consequently, he derived the pygasteroids from regular aulodont echinoids (the Pedinidae), and all other irregular echinoids from stirodonts. Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) derived pygasteroids from among the Pedinidae, and proposed a stirodont ancestor for the Microstomata in which the lantern is absent (Mintz, 1968). Hess (1971) also classified the keeled teeth of *Holectypus* as of stirodont affinity, but Philip (1965) suggested an aulodont origin for the lantern of holectypoids, which he derived from the Diadematidae. However, Philip (1965) did not give an opinion on the origin of other irregular echinoids. Märkel (1978) presented independent origins for the three irregular orders that possess a lantern, namely: the Cassiduloida Claus, 1880, the Holectypoida Duncan,

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1889, and the Clypeasteroida Agassiz, 1872. Jensen (1981), founding her position on the study of teeth microstructure and ambulacral composition, grouped the orders Pygasteroida and Pedinoida Mortensen, 1939 (aulodont regular echinoids) into the superorder Pedinaceae. She made this the sister group of all other irregular echinoids, which then constitute a monophyletic assemblage.

The hypothesis of the polyphyletic origin of irregular echinoids was first challenged by Kier (1974), who showed that the morphology of the lantern and teeth is similar in the genera *Pygaster* and *Holectypus*, but he did not draw any conclusions about their origin. Smith (1981) showed that all irregular echinoids possess the same type of lantern with diamond-shaped teeth, a type already present in a 'regular' species (*Eodiadema* aff. *minutum* (Buckman, 1845) *in* Strickland & Buckman, 1845) which was in turn related to aulodont echinoids. He also considered the genera *Pygaster* and *Holectypus* to be closely related and to constitute the sister group of all other Irregularia. Smith's view has been followed by successive authors (Rose, 1982; Rose & Olver, 1988; Anzalone, Teruzzi & Smith, 1999; Smith & Anzalone, 2000; Solovjev & Markov, 2004).

Basically, all previous works on the origin of irregular echinoids rely on the study of the four following characters: (1) the position of the periproct with respect to the apical system; (2) the Aristotle's lantern; (3) tubercle crenulation; and (4) the organization of ambulacral plates. Depending on each author and their views of a character's relative importance, these characters have fomented arguments both for and against the unique origin (that is, the monophyly) of irregular echinoids. However, Kier's (1974) and Smith's (1981, 1982) findings that the irregulars are monophyletic based on lantern morphology are seldom questioned.

Even if the monophyly of Irregularia is no longer challenged, a broader definition of irregularity taking into account all of the above-mentioned features is needed. In addition, phylogenetic relationships among irregular taxa as well as the relationship with regular echinoids remain imprecise. Clarification of phylogenetic relationships is an essential stage of understanding the processes by which irregularity is achieved. Through this understanding, a much better picture will develop of the most important radiation of post-'Palaeozoic' echinoids.

2. Materials and methods

2.a. Taxon selection

Fossil taxa are of extreme interest when trying to resolve phylogenies because they bear morphological information of phylogenetic significance that is often absent in extant taxa (Benton, Wills & Hitchin, 2000; Wagner, 2000; Smith, 2001). Moreover, extant taxa are sometimes so different morphologically, when evolution has been rapid enough to accumulate large numbers of apomorphies along a given lineage, that comparisons only among extant forms can be misleading. Uncovering phylogenies necessitates the study of intermediate morphologies, and these are often inherent in the fossil record (Rieppel, 1994).

In the Lower Jurassic, the very earliest irregular echinoids, such as '*Plesiechinus*' *hawkinsi* Jesionek-Szymanska, 1970 (Sinemurian of Nevada) and *Loriolella ludovicii* Meneghini, 1867 (Pliensbachian of Italy), still display the pattern observed in regular echinoids, namely a periproct enclosed by the genital and ocular plates (Jesionek-Szymanska, 1970; Smith & Anzalone, 2000). However, the periproct becomes displaced from the centre of the apical system (becomes more eccentric) during growth and tends to 'stretch' the genital plate in interambulacrum 5 and adjacent ambulacral oculars of the apical system in which the periproct is enclosed. By definition, these genital and ocular plates become posterior elements of the apical system. In later forms, such 'stretching' culminates in disruption of the ring of apical plates and actual migration of the periproct away from the apical system. This trend appears to be progressive over a large span of time ranging from Early Jurassic to Late Jurassic times, and exocyclism therefore appears to have been achieved gradually in irregular echinoids (Jesionek-Szymanska, 1963; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966). By contrast, in Recent irregular echinoids, periproct migration begins during early ontogeny before the closure of the apical system, and posterior plates show little or no evidence of elongation (Gordon, 1926). Therefore, apical structures of the first irregulars are very informative; they display the intermediate patterns lacking even in the early ontogeny of extant forms, and are therefore essential to the comprehension of the processes of periproct migration, and to determine if these processes are homologous in all irregulars.

Homoplasy in morphological characters is a common feature of invertebrate phylogenies (Moore & Willmer, 1997; Wills, 1998). They sometimes constitute evidence for the adaptation of species to similar habits and habitats (Stewart, 1993; Suter, 1994). At other times, they are evidence that hypotheses of homology among the characters in question require reassessment. Phylogenies of echinoids are no exception, and parallel evolution in apical structure has been stressed by several authors (Jesionek-Szymanska, 1963; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Kier, 1974; Saucède, Mooi & David, 2003; Solovjev & Markov, 2004), and more generally for numerous traits within the Cassiduloida (Kier, 1962, 1966; Suter, 1994; Smith, 2001; Wilkinson, Suter & Shires, 1996). The probability of homoplasy increases if too many fossil taxa are selected over too long

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Table 1. List of species used for character coding

Taxon	Stratigraphic range	Collection
Caenocidaris cucumifera (Agassiz, 1840)	Upper Toarcian–Upper Bajocian	Gras, Saucède
Acrosalenia hemicidaroides Wright, 1851	Bajocian–Lower Callovian	Saucède
Farquharsonia crenulata Kier, 1972	Bathonian	
Diademopsis bowerbankii Wright, 1851	Hettangian–Sinemurian	
Eodiadema minutum (Buckman, 1845) *in* Strickland & Buckman, 1845	Upper Sinemurian–Lower Pliensbachian	
Atlasaster jeanneti Lambert, 1937	Sinemurian	Collignon
'*Plesiechinus*' *hawkinsi* Jesionek-Szymanska, 1970	Upper Sinemurian	
Plesiechinus ornatus (Buckman, 1845) *in* Strickland & Buckman, 1845	Aalenian–Bajocian	Clavel, Lambert, UB
Pygaster gresslyi Desor, 1842	Middle Oxfordian–Upper Tithonian	Clavel, Cotteau, Courville, UB, Lambert
Pileus hemisphaericus Desor, 1856	Oxfordian	Lambert, Votat
Holectypus depressus (Leske, 1778)	Bathonian–Callovian	CAS, Cassel, UB, Votat
Loriolella ludovicii (Meneghini, 1867)	Lower Domerian	
Eogaleropygus microstoma (Lambert, 1933)	Middle Toarcian	
Galeropygus agariciformis (Wright, 1851)	Upper Toarcian–Bathonian	UB, UCMP
Hyboclypus caudatus Wright, 1851	Bajocian–Bathonian	Courville, Dailly, Dudicourt, UB
Centropygus petitclerci Lambert, 1901	Upper Aalenian	Clavel
Clypeus plotii Leske, 1778	Upper Bajocian–Lower Callovian	CAS, Courville, Dudicourt, Mooi, UCMP
Pygurus depressus Agassiz *in* Agassiz & Desor, 1847	Bathonian–Upper Callovian	Collignon
Nucleolites clunicularis (Phillips, 1829)	Bathonian–Lower Callovian	Courville; UCMP
Pseudosorella orbignyana Cotteau, 1855	Middle Oxfordian–Lower Tithonian	Lambert
Menopygus nodoti (Cotteau, 1859)	Bathonian	Clavel, Collignon, Cotteau, Dudicourt
Pyrinodia guerangeri (Cotteau, 1862)	Bajocian	
Infraclypeus thalebensis Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891	Tithonian	Courville, Enay, Clavel
Desorella elata (Desor, 1847) *in* Agassiz & Desor, 1847	Upper Oxfordian	Lambert
Pachyclypus semiglobus (Münster, 1829) *in* Goldfuss, 1826–1844	Lower Kimmeridgian	Lory
Orbigniana ebrayi (Cotteau, 1874)	Upper Bajocian	Clavel, Lambert
Pygorhytis ringens (Agassiz, 1839)	Upper Bajocian–Middle Callovian	UCMP, UP
Cyclolampas kiliani (Lambert, 1909)	Upper Bajocian	Fournier
Pygomalus ovalis (Leske, 1778)	Upper Bajocian–Middle Bathonian	Thierry
Collyrites elliptica (Lamarck, 1791) *in* Bruguière, 1816	Upper Bathonian–Upper Callovian	Gras, UB
Disaster moeschi Desor, 1858	Callovian	
Metaporinus sarthacensis Cotteau, 1860	Upper Bathonian–Middle Callovian	Votat
Tithonia praeconvexa Jesionek-Szymanska, 1963	Upper Callovian	Clavel, UCMP

Location of consulted collections: Caillet – Claude Bernard University, Lyon; Collignon – Bourgogne University, Dijon; Cotteau – Claude Bernard University, Lyon; Courville – University of Rennes; Dailly – Claude Bernard University, Lyon; Dudicourt – University of Rennes; Enay – Claude Bernard University, Lyon; Fournier – Joseph Fourier University, Grenoble; Gras – Museum of Grenoble; Lambert – Museum National d'Histoire Naturelle (MNHN), Paris; Lory – Museum of Grenoble; Saucède – Joseph Fourier University, Grenoble; Thierry – Bourgogne University, Dijon; Votat – University of Rennes; CAS – California Academy of Sciences, San Francisco; UB – Bourgogne University, Dijon; UCMP – University of California Museum of Paleontology, Berkeley; UP – University of Poitiers.

an interval of time (Sanderson & Donoghue, 1989; Suter, 1994; Smith, 2001) or if the selected terminal taxa are too distant from the origination time of the group. These problems foster the phenomena of long branch attraction and character exhaustion (Wagner, 1995, 2000). The alternative is a careful selection of taxa relevant to the question and from key time intervals (Stewart, 1993; Smith, 2001).

Taxa used in the present study were chosen exclusively from the Jurassic. In fact, they originate as close as possible to the lowermost Jurassic, the supposed earliest occurrence of irregular echinoids. Therefore, representatives of the orders Spatangoida Claus, 1876, Holasteroida Durham & Melville, 1957 (*sensu* Smith, 1984), Clypeasteroida, Oligopygoida Kier, 1967 and Neolampadoida Philip, 1963 were not considered in the analysis, as they originated in the Early Cretaceous and the Palaeogene (Kier, 1962, 1974; Smith, 1984, 2004; Eble, 1998, 2000; Mooi, 1990; Jeffery, 2001; Villier *et al.* 2004). In a recent study (Barras, in press), certain Jurassic irregular echinoids are included within the orders Spatangoida and Holasteroida. Pending further investigations, we will follow herein the definition of these orders as formulated by Smith (1984).

Taking into account the taxonomic level of the analysis, we selected 33 species representative of 32 genera covering the morphological range expressed during the Jurassic part of the radiation (Table 1). The selection was performed according to availability of material, quality of preservation (with the intention of minimizing missing data), and stability of taxonomic nomenclature. Poorly known genera or those judged to be so similar as to be almost synonymous with other genera were not included.

To resolve the origin of irregular echinoids and to test their monophyly, four species have been selected among 'regular' echinoids to represent the possible stem groups of irregular echinoids as suggested by previous authors. *Diademopsis bowerbankii* Wright,

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Table 2. Data matrix

Characters	1	/6	/11	/16	/21	/26	/31	/36
Caenocidaris cucumifera	00000	00000	00000	00000	00020	01000	00010	0000
Acrosalenia hemicidaroides	00010	00100	01000	00210	00000	00000	00010	2000
Farquharsonia crenulata	00010	00000	01000	00200	00000	00000	000?0	1000
Diademopsis bowerbankii	??0?0	00?00	0?000	00100	00000	00010	10000	1000
Eodiadema minutum	??0?0	00?00	00000	00100	00000	00000	00000	3100
Atlasaster jeanneti	00010	00000	01000	00110	00000	00010	100?0	??00
'Plesiechinus' hawkinsi	11010	00?00	01010	00101	00000	00120	001?0	3101
Plesiechinus ornatus	11021	00011	01010	10300	00000	00120	01110	3101
Pygaster gresslyi	11021	00011	03010	10301	00000	00120	01110	3102
Pileus hemisphaericus	10021	00011	13010	10301	00000	00220	111?0	3100
Holectypus depressus	10021	00011	13012	00301	00000	00120	01100	3101
Loriolella ludovicii	?10??	00??0	01010	11000	10011	01100	00001	??01
Eogaleropygus microstoma	?101?	00??0	01000	10011	1002?	00221	??1?1	3111
Galeropygus agariciformis	01011	00110	01000	21011	1011?	10221	02101	3112
Hyboclypus caudatus	01011	00110	01000	21011	10022	10221	02101	3121
Centropygus petitclerci	11111	00111	02000	21012	1012?	10221	02101	3101
Clypeus plotii	11111	00001	03000	21012	1012?	10221	02101	3102
Pygurus depressus	10121	00001	13002	11012	10122	10221	02101	3102
Nucleolites clunicularis	11111	02011	13000	21022	1012?	10221	02101	3121
Pseudosorella orbignyana	11121	00001	13000	21022	1012?	00221	02101	3111
Menopygus nodoti	01011	00110	01000	20000	00012	00221	021?1	??01
Pyrinodia guerangeri	000?1	00111	13000	0?000	000??	00221	0?1?1	??21
Infraclypeus thalebensis	000?1	01111	12002	11001	00121	00221	021?1	??01
Desorella elata	000?1	01111	12001	11000	00111	00221	0?1?1	??21
Pachyclypus semiglobus	000?1	00011	13001	0?00?	00???	00221	021?1	??21
Orbignyana ebrayi	01011	10110	02100	21010	1002?	10221	02101	??21
Pygorhytis ringens	01111	00100	02101	11011	10021	10221	02101	??21
Cyclolampas kiliani	01111	20100	02101	01010	1002?	11221	02101	??22
Pygomalus ovalis	11111	20010	02100	10020	10022	10221	02101	??20
Collyrites elliptica	11111	21011	12101	01021	11022	10221	02101	??21
Disaster moeschi	11111	00000	03101	00000	1102?	11221	02101	??21
Metaporinus sarthacensis	10111	00001	12101	00021	1102?	10221	02101	??20
Tithonia praeconvexa	01111	00000	02101	00020	11021	10221	02101	??20

Character states are described in the text.

1851 was chosen as the earliest representative of the Diadematacea Duncan, 1889. The genus appeared as early as the end of the Triassic (Bather, 1911; Kier, 1977; Smith, 1988) and is considered a representative of the stem group from which all the Irregularia and Stirodonta Jackson, 1912 originated (Smith, 1981). The Aristotle's lantern of *D. bowerbankii* was precisely described by Hawkins (1934), and is among the oldest known of the aulodont type (Kier, 1974; Jensen, 1981). The species *Acrosalenia hemicidaroides* Wright, 1851 was selected as the representative of the Stirodonta, which has been considered a possible ancestor for certain groups of, or for all, the irregular echinoids (Durham & Melville, 1957; Melville, 1961; Durham, 1966; Jesionek-Szymanska, 1963; Mintz, 1968). The genus *Acrosalenia* Agassiz, 1840 appeared as early as the Early Jurassic (Jensen, 1981), and is thought to contain the first stirodonts. The family Acrosaleniidae Gregory, 1900 is characterized by an eccentric periproct and the presence of one or several supplementary plates in the apical system (Fell, 1966). *Farquharsonia crenulata* Kier, 1972 belongs to the family Diadematidae, which has been considered the possible stem group of holectypoids (Mortensen, 1948; Philip, 1965), pygasteroids (Hawkins, 1912, 1922), galeropygoids (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) or of all the Irregularia (Jesionek-Szymanska, 1963; Smith, 1981). *F. crenulata* is characterized by an eccentric periproct within the apical system. Finally, *E. minutum* has been placed as the sister group of the Irregularia (Smith, 1981, 1984). *Caenocidaris cucumifera* (Agassiz, 1840), a representative of Cidaroidea Claus, 1880, was chosen as outgroup to root the trees. The Cidaroidea diverged from other post-'Palaeozoic' echinoids as early as the end of the Triassic (Kier, 1974, 1977; Smith, 1981, 1990).

2.b. Character coding

The high taxonomic level of the analysis required a selection only of characters relevant to the question under consideration (as recommended by Stewart, 1993), that is, early evolution of the major irregular taxa. Therefore, selected characters deal with general structures of the test common to all taxa in the analysis, and are not subject to variation at the species level.

A set of 39 characters was coded (Table 2) and organized into the following four main categories, which are themselves broken down into subcategories that deal with specific features within some of these categories. (1) The first 16 characters concern the apical system, the periproct and the relationships between both structures. Character coding relies partly on

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the interpretation of apical disruptions and periproct migration according to the Extraxial-Axial Theory (e.g. character 3), a model that is general enough to allow comparison between morphologically distant taxa (such as regular and irregular echinoids). (2) The next 18 characters (17–34) deal with structures of the corona, including the ambulacra, interambulacra, peristome, tuberculation and spines. (3) Three characters (35–37) concern the Aristotle's lantern. (4) The last two characters (38, 39) deal with the overall shape of the test.

2.c. Tree computing methods

We used the software PAUP 4.0b10 (Swofford, 2000) to perform a parsimony analysis. Because of the large size of the data matrix (Table 2), trees were computed using the heuristic search algorithm and the ACCTRAN optimization criterion. Character states were unordered. One hundred replicates with random taxon addition sequences were performed to make sure that the taxon addition order used by software PAUP 4.0b10 does not hinder the discovery of other trees of shortest length. Parsimony indices were also obtained with PAUP 4.0b10, and indices of stratigraphic congruence were computed with the software GHOSTS 2.4 (Wills, 1999*b*). Three indices of stratigraphic congruence were calculated: Stratigraphic Consistency Index (SCI: Huelsenbeck, 1994), Relative Completeness Index (RCI: Benton, 1994), and Gap Excess Ratio (GER: Wills, 1999*a*) tests for index values were computed by randomization according to the procedure described in the software GHOSTS 2.4 (Wills, 1999*b*).

2.d. Character analysis

2.d.1. Genital and ocular plates (characters 1–5)

Plate columns and, in some cases, even individual plates making up the test of a given sea urchin can be homologized to those of any other urchin. A numbering system based on the cycle of radii and interradii around the peristome was devised by Lovén (1874) as summarized in David, Mooi & Telford (1995) to refer precisely to specific plates and plate columns. We use this system to identify specific plates in the apical system and the coronal skeleton. Also, to save space, we often omit the term 'plate' in reference to a specific element. For example, 'genital plate 2' can be abbreviated to 'genital 2'.

Genital 2 (which contains the madreporite) is differentiated from other genital plates by the presence of tiny, often numerous, pores (the hydropores) (Fig. 2a) that lead to the stone canal and thereby to the ring canal of the water vascular system. In 'regular' echinoids, genital 2 is roughly the same size as other genital plates (Fig. 2b). In irregular echinoids, genital 2 tends to increase in size in correlation with the degree to which hydropores are developed (Fig. 2c) (Kier, 1974). Finally, in some irregular echinoids, genital 2 expands so much that it completely separates oculars I and II and genital 1 on one side from oculars III–V and genitals 3 and 4 on the other (ethmolytic apical systems) (Durham & Wagner, 1966) (Fig. 2d).

In some forms, periproct migration is accompanied by a stretching of posterior apical plates, namely genital 5 and ocular plates I and V (Fig. 2e). Posterior oculars are stretched considerably to maintain contact between the periproct and the apical system, but they regain something close to their original shape in taxa whose periproct is completely dissociated from the apical system (Fig. 2a). Genital 5 is the most distorted plate as the periproct moves away from the apical system. In the first irregulars, this extraxial plate is crushed between the posterior rim of the periproct and the axial plates of interambulacrum 5 (Fig. 2e). Subsequently, the plate is progressively incorporated into the periproctal area, and it finally atrophies and almost disappears in more derived forms (Jesionek-Szymanska, 1959, 1963). Gordon (1926) showed that in some extant irregulars, genital 5 is present but extremely reduced in size among the scales of the periproctal membrane.

According to previous authors, the apical system of pygasteroids should be distinguished from that of other irregular echinoids by non-elongated posterior oculars and by the absence of genital 5 incorporated to the posterior rim of the periproct (Hawkins, 1912; Jesionek-Szymanska, 1963; Smith, 1981, 1984). However, this is contradicted by personal observations of different species (*Plesiechinus ornatus* (Buckman, 1845) *in* Strickland & Buckman, 1845; *Pygaster trigeri* Cotteau, 1857 *in* Cotteau & Triger, 1855–1869; *Pygaster laganoides* Agassiz, 1839; *Pygaster joleaudi* Besairie & Lambert *in* Lambert, 1933*a*; *Pygaster umbrella* Agassiz, 1839 and *Pygaster gresslyi* Desor, 1842) showing that posterior oculars are really elongated in these species (Fig. 2f), and that genital 5 can be present on the posterior rim of the periproct, as observed in a juvenile specimen of *P. trigeri* (Bathonian of Sarthes, France; collection of Votat). This supports Gordon's (1926) hypothesis that genital 5 is incorporated into the periproctal area in all irregular echinoids. Perforated by a gonopore in regular echinoids, genital plate 5 loses the gonopore in the first irregulars (but it is still present in '*P.' hawkinsi*) when the plate begins to be distorted. A fifth gonopore reappears several times in the evolutionary history of irregular echinoids: in the Cretaceous holectypoids and in at least three separate clades in the Cenozoic clypeasteroids.

In endocyclic echinoids, whether 'regular' or irregular, posterior ocular plates are separated by the periproct and genital plate 5 (Fig. 2b). In exocyclic echinoids, periproct migration out of the apical system leaves a 'free space' within the apical ring, which is filled either by additional plates or by the rearrangement of standard apical plates according to various patterns that depend on the taxa considered. Posterior oculars are separated by supplementary plates in stem irregulars (Fig. 2g), but are brought closer and finally contact each other in more derived taxa (Fig. 2h). However, in ethmolytic apical structures, posterior oculars do not come into contact because genital plate 2 is extended posteriorly between them (Fig. 2d). The extension of genital plate 2 is independent of periproct migration. Therefore, the separation of posterior oculars was coded in different ways depending on whether they are separated by supplementary plates or by genital plate 2.

1. Development of the genital plate 2: 0, all genital plates of nearly the same size; 1, genital 2 enlarged.
2. Elongation of posterior ocular plates: 0, posterior ocular plates short; 1, posterior ocular plates elongated (much longer than wide).

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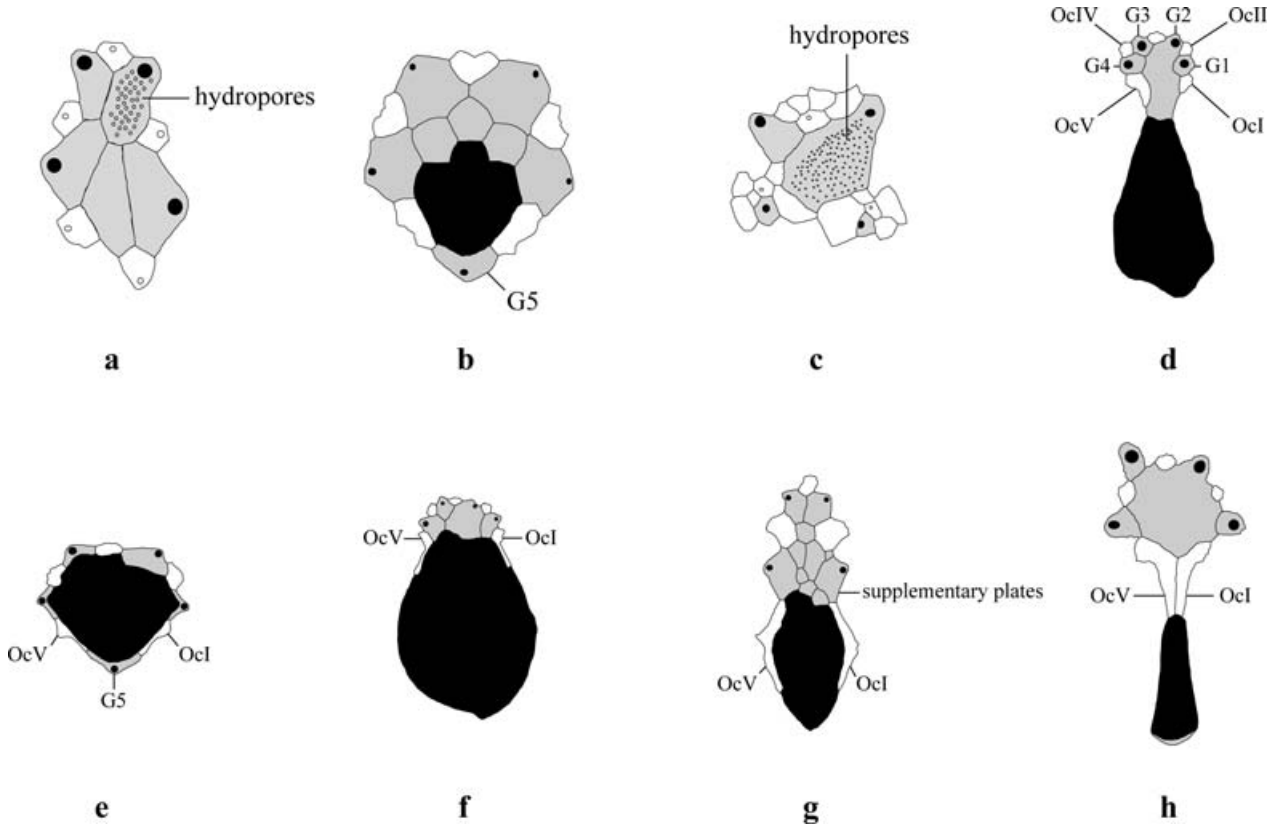


Figure 2. Characters involving genital and ocular plates. (a) *Pachyclypus semiglobus*: hydropores are not widespread and genital 2 is approximately of the same size as other genital plates; posterior oculars do not contact the periproct and are not elongated. (b) *Acrosalenia hemicidaroides*: all genitals have the same size, genital 5 excepted. (c) *Metaporinus sarthacensis*: hydropores are widespread and genital 2 is the largest genital plate. (d) *Pseudosorella orbignyana*: in ethmolythic apical systems, apical plates are separated by the significant extension of genital 2. (e) '*P.' hawkinsi*: posterior oculars and genital 5 are elongated, and genital 5 is 'crushed' between the axial plates of the corona and the periproct. (f) *Pygaster gresslyi*: posterior ocular plates are elongated. (g) *Hyboclypus caudatus*: posterior oculars are separated from each other by the periproct and supplementary plates. (h) *Clypeus plotii*: posterior ocular plates are in contact with each other.

3. Contact between posterior ocular plates: 0, ocular plates completely separated by the periproct or by supplementary plates; 1, ocular plates in contact (or separated by genital plate 2 in ethmolytic apical structures).
4. Development of genital plate 5: 0, genital plate 5 well developed and not deformed; 1, genital plate 5 crescent-shaped, lying at the lower side of the periproct; 2, genital plate 5 lacking or reduced.
5. Perforation of genital plate 5: 0, genital plate 5 bearing a gonopore; 1, genital plate 5 not bearing a gonopore.

2.d.2. Supplementary plates (characters 6–9)

In all Jurassic irregular taxa, the breakout and migration of the periproct is associated with formation of supplementary (or complementary) plates inside the apical system. Supplementary plates first appear in the fossil record in the genus *Galeropygus* Cotteau, 1856 (the earliest, known species of *Galeropygus* is *Galeropygus lacroixi* Lambert, 1924 from the Upper Pliensbachian, but the type specimen appears to be missing from Lambert's collections; the earliest, preserved apical system is from *G. agariciformis* (Wright, 1851) from the Upper Toarcian), and they progressively disappear in all taxa during the Late Jurassic, once the periproct and the apical system are completely separated (except in holectypoids). Contrary to some previous descriptions (Jesionek-Szymanska, 1963; Fell, 1966), and in spite of their infrequent preservation, we have found supplementary plates in pygasteroids (Hawkins, 1944) and in holectypoids (Fig. 3a). The apical system of *Holectypus* has long been interpreted to be composed of five genital plates, the fifth genital plate lacking a gonopore in the Jurassic (Wagner & Durham, 1966). However, considering the apical disruptions induced by periproct migration, and the presence of two or three supplementary plates in the species *Holectypus hemisphaericus* Desor *in* Agassiz & Desor, 1847, it seems more likely that the fifth imperforate 'genital' plate of *Holectypus* and *Pileus* Desor, 1856 is a supplementary plate. The term 'genital' used by most authors actually refers to a function recovered by Cretaceous holectypoids (the plate is again perforated by a gonopore (Wagner & Durham, 1966)), and does not refer to a homology with the posterior genital 5 of other taxa. Supplementary plates are also present in some 'regular' taxa (e.g. Acrosaleniidae) characterized by a very eccentric position of the periproct within the apical system (Fig. 3b).

Supplementary plates are formed inside the apical system. They do not originate in contact with ocular plates, they generally present no precise structural pattern, and they

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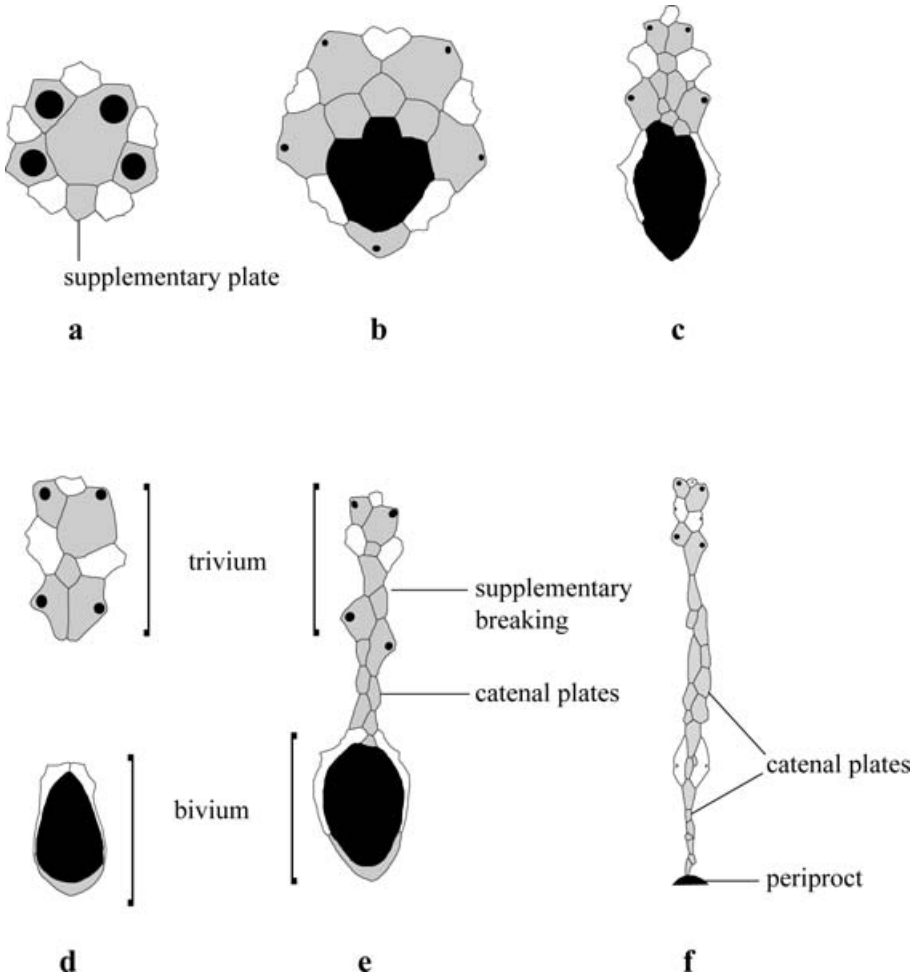


Figure 3. Characters involving supplementary plates. (a) *Holectypus depressus*: genital plate 5 is replaced by a supplementary plate. (b) *Acrosalenia hemicidaroides*: the 'regular' family Acrosaleniidae is characterized by the presence of several supplementary plates in the anterior part of the apical system. (c) *Hyboclypus caudatus*: supplementary plates fill the space created by periproct migration. (d) *Pygorhytis ringens*: in the first Atelostomata, the apical system is broken into an anterior part (trivium) and a posterior part (bivium). (e) *Orbigniana ebrayi*: a supplementary rupture is present within the trivium. (f) *Collyrites elliptica*: catenal (supplementary) plates are present between the trivium and the bivium as well as between the bivium and the periproct.

are variable in size and number irrespective of specimen size. In view of their pattern and position with respect to other apical plates, we consider supplementary plates as elements of the extraxial skeleton. They are present either in the anterior or posterior part of the apical system, and generally fill the free space created by the departure of the periproct (Fig. 3c). In Jurassic Atelostomata, the stretching of the apical system results in breakage into an anterior sub-unit, the trivium (composed of three ocular and four genital plates), and a posterior sub-unit, the bivium (composed of two ocular plates) (Fig. 3d). These two sub-units are connected by a row of supplementary plates, called catenal plates (Durham & Wagner, 1966), and aligned along the III-5 axis in certain taxa (*Orbigniana ebrayi* (Cotteau, 1874) *in* Gotteau, Péron & Gauthier, 1873–1891; *Cyclolampas kiliani* (Lambert, 1909)) (Fig. 3e). Supplementary plates may also link posterior oculars to the periproct (e.g. in *Infraclypeus* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891 and *Collyrites* Desmoulins, 1835). In this case, we assign the term catenal to these plates as well (Fig. 3f).

6. Supplementary plates between the bivium and the trivium: 0, no supplementary plates between the bivium and the trivium; 1, supplementary plates in continuous row of catenal plates between the bivium and the trivium; 2, supplementary plates in irregular plating between the bivium and the trivium.
7. Supplementary plates between the posterior ocular plates and the periproct: 0, no supplementary plates between the posterior ocular plates and the periproct; 1, supplementary plates forming a catenal row between the posterior ocular plates and the periproct; 2, supplementary plates in irregular plating between the posterior ocular plates and the periproct.
8. Supplementary plates between the anterior ocular plates: 0, no supplementary plates between the anterior ocular plates; 1, supplementary plates present between the anterior ocular plates.
9. Supplementary plates between the posterior ocular plates: 0, no supplementary plates between the posterior ocular plates; 1, supplementary plates present between the posterior ocular plates.

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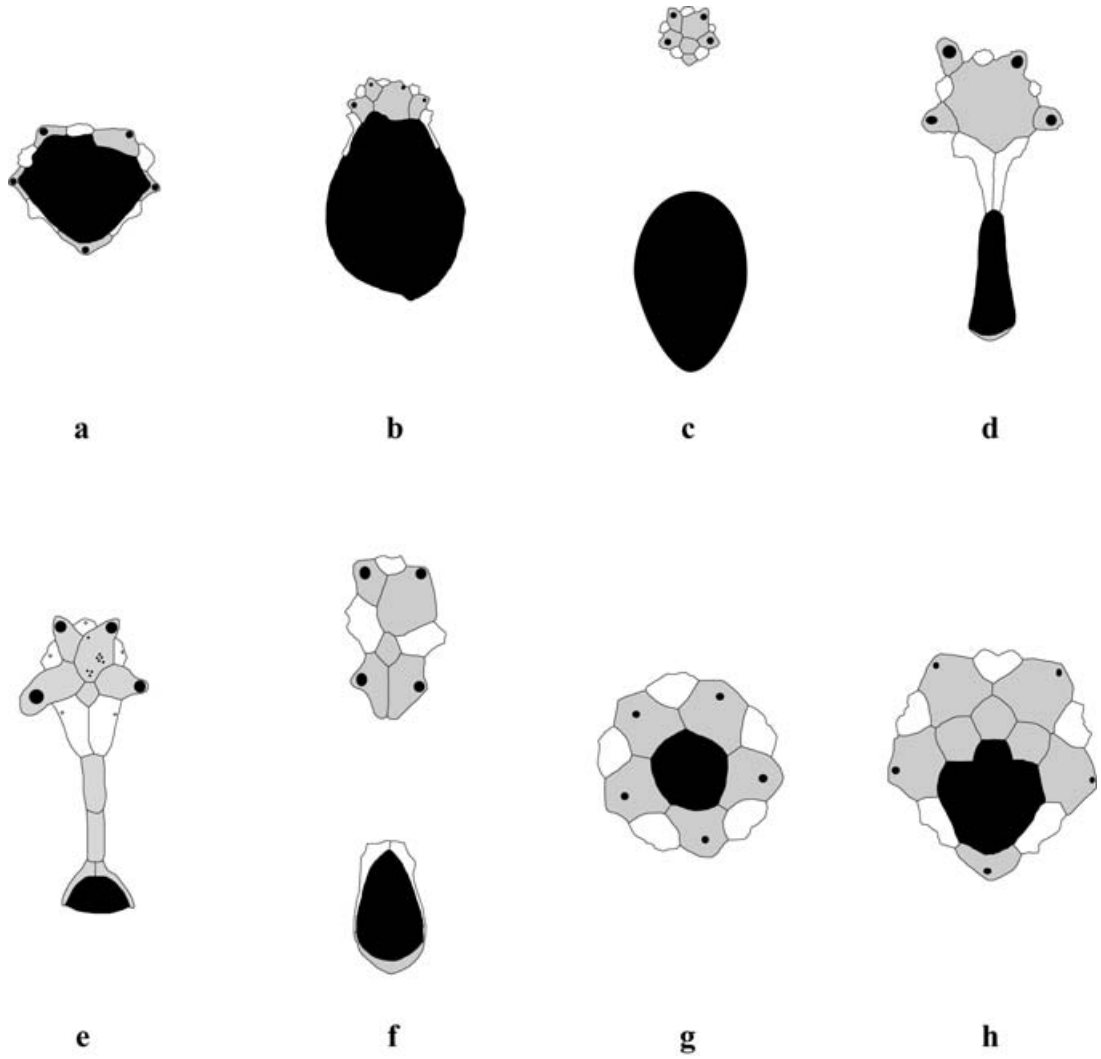


Figure 4. Relationships between the periproct and the apical system. (a) *'Plesiechinus' hawkinsi*: the periproct is still enclosed within the apical system, but posterior apical plates are stretched by the onset of periproct migration. (b) *Pygaster gresslyi*: posterior ocular plates are elongated but do not contact genital 5, the apical system is exocyclic. (c) *H. hemisphaericus*: the periproct is isolated within the axial plates of the corona. (d) *Clypeus plotii*: posterior oculars still contact the periproct but the anterior apical plates are already grouped together. (e) *Nucleolites clunicularis*: posterior oculars do not contact the periproct and the apical plating forms a compact structure. (f) *Pyrorhytis ringens*: the apical plating of the trivium forms an intercalary structure. (g) *Caenocidaris cucumifera*: the apical plating forms a dicyclic structure. (h) *Acrosalenia hemicidaroides*: the apical plating forms a hemicyclic structure.

2.d.3. Relationships between periproct and apical system (characters 10–13)

In 'regular' echinoids, two distinct patterns in apical structure can be recognized: (1) they are said to be dicyclic when genital and ocular plates form two concentric circles around the periproct, with no ocular joining the periproctal rim (Fig. 4g), and (2) they are monocyclic or hemicyclic when at least some ocular plates form part of the inner circle around the periproctal rim (Fig. 4a, h) (Durham & Wagner, 1966).

Durham & Melville's (1966) definition of exocyclism (that is, tests with the periproct located outside the apical system) is not precise enough to be applied to early irregular echinoids which are characterized by apical structures intermediate between the common endocyclic and exocyclic systems. Therefore, we refine Durham & Melville's (1966) definition of exocyclism as the contact between the periproct and the axial plates of interambulacrum 5. This contact is made possible by the breaking of the apical rim (between posterior oculars and genital 5) and the periproct's movement out of the apical circle (as suggested by the term exocyclism).

Exocyclism is realized progressively in many taxa (Jesionek-Szymanska, 1963), first by the breakage between the posterior oculars and genital 5, then by the progressive movement of the periproct away from posterior oculars which stretch before losing all contact with the periproct (Fig. 4c, d). Once they lose this contact, apical plates begin to group together and fill the space created by periproct removal. Therefore, apical plates begin to group together in the anterior part of the apical system, even when the periproct is still in contact with posterior ocular plates (Fig. 4e). This pattern is present in Cassiduloida and basal Atelostomata. Then, posterior ocular plates tend to group together with the anterior part of the apical system once they lose contact with the periproct (Jesionek-Szymanska, 1963; Thierry, 1974) (Fig. 4e). Finally, exocyclism results in the isolation of

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the extraxial periproct embedded within a growth zone boundary, between the axial plates of interambulacrum 5 and distant from other extraxial elements (that is, the genitals) (Fig. 4c).

The grouping of apical plates is achieved in two different ways, leading to two types of apical patterns: (1) the intercalary (or elongate) structure (Fig. 4f) in which genital plates 1 and 4 are not in contact with the periproct, and genital plate 2 does not contact genital plate 4; and (2) the compact structure (Fig. 4d, e) in which genital plates 1 and 4 are not in contact with the periproct, and genital plate 2 contacts genital plate 4.

10. Endo- and exocyclism: 0, periproct not in contact with interambulacrum 5 (endocyclic state); 1, periproct in contact with the interambulacrum 5 (exocyclic state).
11. Contact between the posterior ocular plates and the periproct: 0, periproct in contact with the posterior ocular plates (or with the posterior genital plates when the ocular plates are exsert); 1, periproct not in contact with the posterior ocular plates.
12. Structure of the apical system: 0, apical system dicyclic, genital and ocular plates forming two concentric circles around the periproct, no ocular joining the periproctal rim; 1, apical system monocyclic or hemicyclic, at least some ocular plates participate in the inner circle around the periproctal rim; 2, apical system intercalary, genital plates 1 and 4 not in contact with the periproct, and genital plate 2 not in contact with genital plate 4; 3, apical system compact, genital plate 2 in contact with genital plate 4.
13. Disjunction of the apical system: 0, posterior ocular plates and genital plates 1 and 4 in contact; 1, posterior ocular plates and genital plates 1 and 4 disjunct.

2.d.4. *The periproct (characters 14–16)*

The periproct is large in pygasteroids and holectypoids, as well as in *L. ludovicii* (Smith & Anzalone, 2000) (Fig. 5a, b). In these taxa, it occupies a much larger surface than the rest of the apical disc. In contrast, the periproct is relatively smaller in all other irregular echinoids, with a surface area nearly the same size as the rest of the apical disc (Jesionek-Szymanska, 1963) (Fig. 5c, d).

In numerous Jurassic irregulars, the periproct remains on the apical side of the test. This position is described as supramarginal. However, in the majority of menopygids and Atelostomata, the periproct migrates posteriorly to the margin of the test, and is said to be marginal. It can even reach the oral side (as in *Holectypus*, *Pygurus* Agassiz, 1839, and *Infraclypeus* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891) and become inframarginal.

In 'regular' echinoids and holectypoids, the periproct is flush with the test, whereas it is depressed in pygasteroids, in *L. ludovicii* and *Eogaleropygus microstoma* (Lambert, 1933*b*) (Jesionek-Szymanska, 1978; Smith & Anzalone, 2000). The periproct is vertical and located at the bottom of a deep anal groove in galeropygoids, cassiduloids and early atelostomates.

14. Size of the periproct: 0, surface of the periproct smaller than or of nearly the same size as the apical disc; 1, surface of the periproct much larger than the apical disc.

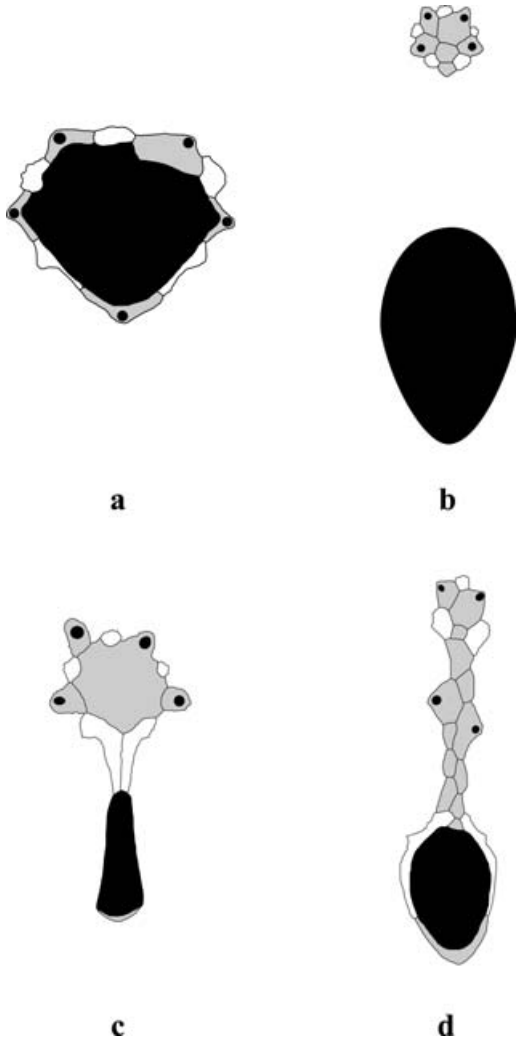


Figure 5. Characters of the periproct. In (a) (*'Plesiechinus' hawkinsi*) and (b) (*Holectypus hemisphaericus*), the periproctal area exceeds the area filled by apical plates. In (c) (*Clypeus plotii*) and (d) (*Orbigniana ebrayi*), the periproctal area is smaller or approximately equals the area filled by apical plates.

15. Position of the periproct: 0, periproct supramarginal; 1, periproct marginal; 2, periproct inframarginal.
16. Attitude of the periproct: 0, periproct flush with the test; 1, periproct in a slight anal groove; 2, periproct vertical and in a steep anal groove.

2.d.5. *Ambulacra (characters 17–21)*

Kier (1974) reviewed the evolution of plate compounding throughout the Mesozoic. Originating in Late Triassic cidaroids, plate compounding diversified gradually during the Mesozoic and corresponds to an increase in the number of elementary ambulacral plates. Kier interpreted the evolution of plate compounding as a mechanism by which echinoids could increase the number of tube feet (sensation, locomotion and food collection), while maintaining the size of ambulacral tubercles and spines (protection against predation). Because of miniaturization of their spines, most irregular taxa are distinguished by simple ambulacral plating, except in pygasteroids and holectypoids which

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retain plate compounding of the plesiechinid type. Jensen (1981) distinguished between the plesiechinid type of plate compounding in Pygasteroida (which she related to the early diadematoid type), from the pattern present in Holectypoida (the holectypid type). This was an argument to make Eognathotomata polyphyletic, but in designating these as separate types and therefore essentially as autapomorphies for each of these groups, Jensen obviated the possibility that they could contain phylogenetic information. Herein, we follow Kier (1974) in considering that holectypoids and pygasteroids share the same type of compounded plates.

Petaloids are absent in the earliest irregular echinoids, although ambulacral pores are slightly elongated in '*P.' hawkinsi*, pygasteroids and holectypoids (Jesionek-Szymanska, 1970). Petaloid ambulacra became strongly developed in cassiduloids (and especially in the genera *Clypeus* Leske, 1778 and *Pygurus*) as early as the Middle Jurassic, with the outer pore of the pore pairs elongated into a narrow slit. Petals were slightly developed later on in Atelostomata, but to a lesser extent. Pore morphology and tube foot morphology are closely linked (Smith, 1978*a*, 1980*a*). Petaloid evolution corresponds to a specialization of aboral tube feet that allows irregular echinoids to conduct gas exchange more efficiently, especially in relation to new living habits such as burrowing, a more intense activity than grazing (Kier, 1974) that also results in reduced exposure to ambient water flow.

The appearance of phyllodes corresponds to an increase in number, specialization and enlargement of adoral ambulacral pores. The function of phyllodes is to enhance efficiency of tube feet for food gathering (particle picking) in irregular echinoids (Telford & Mooi, 1996) or for attachment in 'regular' echinoids. Whatever the function, phyllodes were considered homologous structures in 'regular' and irregular echinoids by Kier (1974). Phyllodes are present in 'regular' echinoids as early as the Early Jurassic (in pedinoids). In pygasteroids, phyllodes are very similar to those of pedinoids. In galeropygoids and first cassiduloids, phyllopodia became larger and arranged in arcs of three. This increase in size and number is correlated with a modification of adoral ambulacral plating (demi-plates and reduced plates) that allows crowding of the pores in the region near the peristome. Phyllode arrangement is used in systematics. For example, the families Clypeidae Lambert, 1898 and Nucleolitidae Agassiz & Desor, 1847 are distinguished according to their phyllopodial patterns (Kier, 1962). Phyllodes are also differentiated in the first Atelostomata which inherited the arrangement of phyllopodes in arcs of three (Jesionek-Szymanska, 1963). However, menopygids have been distinguished from galeropygoids mainly by the absence of phyllodes (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Rose & Olver, 1988).

17. Depression of ambulacra: 0, ambulacra not depressed on the oral side; 1, ambulacra depressed on the oral side.
18. Compounded plates (ambulacral units composed of several elemental plates bound together by a single large primary tubercle): 0, simple ambulacral plating, ambulacra composed throughout of simple plates; 1, compound plating of diadematoid type, unit of three plates bound together; 2, compound plating of acrosaleniid type, a simple plate alternates with two plates bound together; 3, compound plating of plesiechinid type, each plate overlained by two tubercles that bind it to two different units.
19. Structure of the adoral part of the ambulacra: 0, ambulacra composed only of primary plates adorally, that is plates with an adradial (contact with the interambulacral column) and a perradial suture (contact with the neighbouring ambulacral column); 1, ambulacra composed adorally of reduced plates intercalated between primary plates, and pore pairs arranged in triads; 2, ambulacra composed adorally of reduced plates intercalated between primary plates, and pore pairs not arranged in triads.
20. Petals: 0, petals not differentiated, partitioned isopores aborally; 1, petals slightly developed, enlarged and specialized pore pairs aborally; 2, petals well developed, enlarged and elongated anisopores, outer pores in a narrow slit.
21. Phyllodes: 0, phyllodes not differentiated, ambulacral pores not specialized near the peristome; 1, phyllodes with specialized ambulacral pore pairs near the peristome.

2.d.6. Interambulacra (characters 22, 23)

Atelostomata are distinguished from other irregular echinoids by differentiation in the size of their adoral interambulacral plates (Devriès, 1960; Kier, 1974). However, the earliest Atelostomata (*O. ebrayi*, *C. kiliani*, *Pygomalus ovalis* (Leske, 1778) and *Pygorhytis ringens* (Agassiz, 1839)) still lack this differentiation (Jesionek-Szymanska, 1963; Kier, 1974). Such a differentiation first appeared in the Upper Bathonian (as in *Collyrites elliptica* (Lamarck, 1791) *in* Bruguière, 1816) by the enlargement of the first plate of interambulacrum 5, thereby forming the labrum (Jesionek-Szymanska, 1963; Mintz, 1968). For Kier (1974), this differentiation was related to the evolution of heart-shaped tests with wide peristomes in Atelostomata. Very early in ontogeny, the relative positions of interambulacral plates become nearly fixed on the oral side so that test and peristomial growth is almost exclusively accommodated by the enlargement of adoral plates.

Galeropygoids and cassiduloids evolved an outward bulging of the basicoronal interambulacral plates to form the so-called bourrelets. Bourrelets are present, although slightly developed, in certain menopygids as well. As early as the Middle Jurassic, bourrelet development is particularly significant in cassiduloids in which bourrelets intrude into the peristome (e.g. *Clypeus*), and might have been involved in food gathering. These structures are covered by many small tubercles and tiny spines which some have hypothesized were used to push particles up into the peristome (Kier, 1962; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966). However, Telford & Mooi (1996) observed no such function of the bourrelets in extant *Cassidulus* Lamarck, 1801, in which podia were the sole agents of food transfer into the mouth. Spines were never employed in food manipulation, and bourrelet spination was actually moved out of the way to admit particles being manipulated by the phyllopodia.

22. Differentiation of oral interambulacral plates: 0, basicoronal interambulacral plates not differentiated; 1, enlarged basicoronal interambulacral plates.
23. Bourrelets (doming of the interambulacra near the peristome): 0, bourrelets absent; 1, bourrelets present.

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2.d.7. Peristome (characters 24–27)

Buccal notches and the perignathic girdle are structures internal to the peristome and associated with the function of the Aristotle's lantern (Melville & Durham, 1966). They are present in 'regular' echinoids (buccal notches are absent in cidaroids) and in the irregular pygasteroids and holectypoids (Kier, 1974) but disappear as the lantern is lost in the Microstomata. The earliest Microstomata retain relics of buccal notches and of a perignathic girdle as marks of their 'regular' origin. Relics can be found in menopygids (Rose & Olver, 1988), in *L. ludovicii* (Smith & Anzalone, 2000), and in some Atelostomata and galeropygoids (Kier, 1962; Jesionek-Szymanska, 1963).

In Microstomata, the anterior displacement of the peristome accompanies the appearance of bilateral symmetry of the test. Anterior shifting of the peristome can be related to the adoption of burrowing and infaunal living habits that necessitated an exclusive forward motion of echinoids to facilitate the ingestion of particles gathered from the sediment (Kier, 1974).

24. Buccal notches: 0, buccal notches well developed; 1, small residual buccal notches; 2, buccal notches absent;
25. Perignathic girdle (internal processes for attachment of muscles supporting the lantern): 0, perignathic girdle complete; 1, perignathic girdle atrophied, no longer functional; 2, perignathic girdle absent.
26. Position of the peristome: 0, peristome close to a central position; 1, peristome anterior.
27 Depression of the peristome: 0, peristome depressed; 1, peristome flush with the test.

2.d.8. Tubercles and spines (characters 28–34)

Kier (1974) and Smith (1981) observed a trend toward the reduction in size and increase in number of tubercles and spines in the evolution of post-'Palaeozoic' echinoids. The greatest decrease in size of spines occurs with the appearance of irregular echinoids. In the earliest irregular, '*P.' hawkinsi*, tubercles of the oral side are of the same size in ambulacra and interambulacra, whereas the later *L. ludovicii* still retains large interambulacral tubercles and spines (Smith & Anzalone, 2000). Nevertheless, in succeeding irregular echinoids, tubercles and spines are of the same size in ambulacra and interambulacra. The decrease in tubercle size and their correlated increase in number became more pronounced in Microstomata as early as the Pliensbachian, and is noticeable in the genus *Galeropygus* in which there are many more tubercles than in *Plesiechinus* (Kier, 1974, 1982; Smith, 1978*b*). In pygasteroids and holectypoids, tubercles are ordered in concentric rows all over the test. The areoles, depressions around the tubercles for attachment of muscles controlling movement of spines, are asymmetrical around tubercles of the oral side. The asymmetry is radially arranged all over the oral side, so that there is no specialization to accommodate the power stroke by the muscle during movement in a particular direction (Smith, 1980*b*). Conversely, the increase in tubercle number in Microstomata goes along with an unordered arrangement of tubercles on the test, but the asymmetry of areoles is organized in accordance with the bilateral symmetry of the test and is a specialization for forward and unidirectional movement of echinoids. It is related to the adaptation of Microstomata to moving upon or within the sediment in a single direction (Smith, 1978*b*, 1980*b*).

Crenulation, the ribbing or lobation of the perimeter of the tubercle's platform below the mamelon, evolved once but has been lost several times in the evolution of regular echinoids (Lewis & Ensom, 1982). In the Introduction to the present work, it was noted that Mortensen (1948) used the crenulation of tubercles as a criterion to argue for the independent origin of holectypoids and pygasteroids, whereas Jesionek-Szymanska (1970), as well as Rose & Olver (1984), showed that crenulation could not be used to demonstrate the independent origin of these groups. In fact, tubercles are originally crenulated in irregular echinoids, and all the Microstomata have crenulated tubercles (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966).

The internal structure of spines differs among echinoids but is constant in a given species (Hyman, 1955) or even at higher taxonomic levels such as genera or families (Melville & Durham, 1966). The internal structure of spines is used in the systematics of 'regular' echinoids. In particular, some 'regular' taxa evolved solid spines, whereas they are hollow in others as well as in irregular echinoids, excepted in pygasteroids. Hence, pygasteroids possess solid spines, whereas spines are hollow in holectypoids (Smith, 1981).

28. Density of primary tubercles on ambulacral plates: 0, one single large primary tubercle on each ambulacral plate (or compound plate); 1, two or three 'primary' tubercles on each ambulacral plate near the ambitus; 2, numerous 'primary' tubercles on each ambulacral plate near the ambitus.
29. Density of primary tubercles on interambulacral plates: 0, one single large primary tubercle on each interambulacral plate; 1, two or three 'primary' tubercles on each interambulacral plate near the ambitus; 2, numerous 'primary' tubercles on each interambulacral plate near the ambitus.
30. Ordering of primary tubercles: 0, primary tubercles ordered in concentric rows all over the test; 1, primary tubercles not ordered in concentric rows.
31. Crenulation of primary tubercles (tubercles with ribbed periphery): 0, primary tubercles crenulate; 1, primary tubercles smooth.
32. Symmetry of areoles (depression for attachment of muscles supporting and controlling movement of spines): 0, areoles with a radial symmetry on the oral side; 1, areoles with bilateral symmetry, the long axis arranged radially on the oral side; 2, areoles with bilateral symmetry, the long axis arranged anterior to posterior on the oral side.
33. Size of spines: 0, large primary spines; 1, short and slender primary spines.
34. Internal structure of spines: 0, hollow primary spines; 1, solid primary spines.

2.d.9. Aristotle's lantern (characters 35–37)

The importance of the Aristotle's lantern for the systematics of irregular echinoids was discussed in the Introduction. Smith (1981, 1982) showed that irregular echinoids and *E. minutum* evolved diamond-shaped teeth from the aulodont type (grooved teeth) by paedomorphosis (McNamara, 1982). Similarly, *E. minutum*, the holectypoids and juvenile cassiduloids (cassiduloids lose the lantern as adults) have wide

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pyramids derived from the narrow pyramids of aulodont echinoids (e.g. *Diademopsis* Desor, 1855).

35. Presence of the lantern: 0, Aristotle's lantern present in adults; 1, Aristotle's lantern absent in adults.
36. Type of teeth: 0, teeth of cidaroid type; 1, grooved teeth; 2, keeled teeth; 3, teeth diamond-shaped in cross-section.
37. Type of pyramids: 0, narrow pyramids; 1, wide pyramids.

2.d.10. Shape of the test (characters 38, 39)

The choice of coding characters linked to the shape of the echinoid test (profile and outline) in a phylogenetic analysis may seem questionable. Indeed, at a species level, such characters are known to be 'sensitive' to environmental variations (Néraudeau, 1995), and their significance for taxa discrimination may be reproved. For example, in several Cretaceous irregular groups (such as archiaciids, holectypoids and hemiasters), the shape of the test appears related to sediment granulometry, to the depth of burrowing, and to water depth (Nichols, 1959; Smith & Paul, 1985; Zaghbib-Turki, 1989; Néraudeau & Moreau, 1989). However, because of the taxonomic level of the present analysis along with the antiquity and the originality of first irregular echinoids, it seemed relevant to consider the possible phylogenetic significance of test shape. Furthermore, Kier (1974) noted a change in the general shape of the echinoid test with the appearance of irregular echinoids. He correlated this change to the migration of the periproct outside the apical system. Indeed, tests of irregular echinoids can be elongated and display a bilateral symmetry that distinguishes them from 'regular' echinoids (Smith, 1981). However, in earliest irregular echinoids, tests are wider than long and the bilateral symmetry is not so conspicuous (e.g. '*P.' hawkinsi* and *G. agariciformis*). Elongated tests did not appear before the Middle Jurassic in Microstomata. The elongation and bilateral symmetry of the test are related to the adaptation of irregular echinoids to a unidirectional mode of locomotion (Kier, 1974; Smith, 1978*b*, 1981, 1984). Irregular echinoids also evolved flattened tests, particularly pronounced in the cassiduloids *Clypeus* and *Pygurus* (Kier, 1974).

38. Marginal outline of the test: 0, circular outline, length and width of the test more or less equal; 1, widened outline, test wider than long; 2, elongated outline, test longer than wide.
39. Profile of the test: 0, high, rounded test; 1, low, rounded test; 2, low, flattened test.

3. Results

3.a. General results

The parsimony analysis found 156 shortest trees with a length of 151 steps. Completion of 100 replicates with random taxon addition sequences did not reveal the existence of other trees of equal shortest length. We used a majority-rule consensus tree to summarize this set of trees (Fig. 6). Phylogenetic relationships among taxa are almost all resolved, with the exception of two polytomies: one involves the 'regular' echinoids *A. hemicidaroides* Wright, 1851 and *F. crenulata* Kier, 1972 and the other concerns the derived irregular taxa *Clypeus plotii* Leske, 1778, *Pygurus depressus* Agassiz *in* Agassiz & Desor, 1847, *Nucleolites clunicularis* (Phillips, 1829) and *Pseudosorella orbignyana* Cotteau, 1855. Most of the nodes are well supported (Fig. 6); the uncertainties (4 nodes out of 28) lying within the relationships among crown cassiduloids (one node) and atelostomates (three nodes). Parsimony indices (CI = 0.391, RI = 0.738, RC = 0.288, HI = 0.609) fall within the ranges of values obtained in previous cladistic analyses carried out on irregular echinoids (Suter, 1994; Smith & Anzalone, 2000; Smith, 2001, 2004; Villier *et al.* 2004). These recurrent and relatively low values reveal the importance of homoplastic state changes in these phylogenetic analyses of primitive fossil forms (Suter, 1994; Villier *et al.* 2004).

The overall aspect of the majority-rule consensus tree is clearly asymmetric, with a paraphyletic assemblage constituted by stem 'regular' taxa, and a monophyletic group corresponding to the Irregularia (clade 1). The question of whether to include *E. minutum* in the Irregularia or not is discussed below. This monophyletic assemblage is organized into four sub-units corresponding to the four main recognized groups of Jurassic irregulars: the Eognathostomata (clade 2), the menopygids (excluding *Menopygus nodoti* (Cotteau, 1859)) (clade 4), the Neognathostomata Smith, 1981 (clade 5), and the Atelostomata (clade 6). The last three clades are themselves united to form a sixth grouping, the Microstomata (clade 3). The monophyly of Irregularia is well-supported (decay index $\geq$ 3, bootstrap value = 90 %), and departs from Jensen's analysis (1981) but agrees with all other, more recent cladistic works (Smith, 1981, 1984; Rose & Olver, 1988; Smith & Anzalone, 2000; Solovjev & Markov, 2004).

3.b. Main clades

3.b.1. Clade 1

All recognized irregular taxa in the analysis are strongly related and form the clade Irregularia (Fig. 6). The clade is supported by the following synapomorphies: relatively large size of the periproct (character 14), high density of primary tubercles on ambulacral and interambulacral plates (characters 28 and 29), shortening of primary spines (character 33), *L. ludovicii* excepted (characterized by large primary spines attached to a primary tubercle, one to each interambucral plate), and a relatively low test camber (character 39). The relatively large surface area of the periproct is seen in the very first irregulars ('*P.' hawkinsi* and *L. ludovicii*), as well as in the Eognathostomata (Clade 2). However, all other irregulars possess a relatively small periproct. Similarly, a low test profile characterizes basal taxa, but presents numerous reversions in more derived groups. On the contrary, characters related to appendages, namely the increased number of primary tubercles and shortened primary spines (characters 28, 29 and 33), exhibit relatively low levels of homoplasy and are shared both by all basal and terminal irregular taxa (*L. ludovicii* excepted).

The diamond-shaped teeth (character 36) and narrow pyramids (character 37) are states shared by *E. minutum* and

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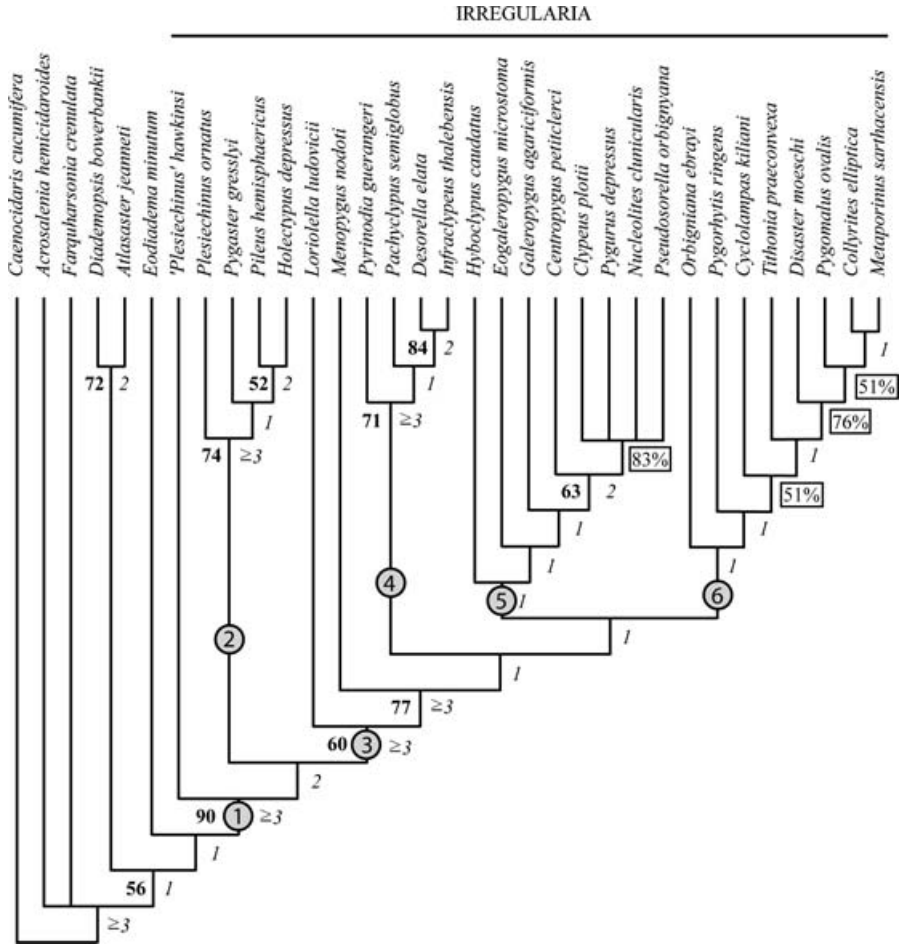


Figure 6. Fifty per cent majority-rule consensus tree of the 156 equally parsimonious cladograms computed from the data matrix of Table 2. *Caenocidaris cucumifera* is the outgroup. Clades discussed in the text are designated by encircled numbers. Four nodes are not fully supported; their support is given as percentage values in squares. Bootstrap values are indicated in bold on the left of each branch; Bremer support values are in italics on the right of each branch.

lantern-bearing irregulars (Smith, 1981), and are features that led Smith (1984) to include *E. minutum* in the Irregularia. *E. minutum* shares two other characters with irregular echinoids: the elongation of posterior ocular plates (character 2) and the development of genital plate 2 (character 1). However, these two characters show important homoplastic changes within the Irregularia (Fig. 7).

'P.' hawkinsi shares the apomorphic characters of other irregular taxa: a relatively large periproct (character 14), and specialization of appendages (characters 28, 29 and 33). Previous authors (Jesionek-Szymanska, 1970; Smith, 1981; Kier, 1982) also considered *'P.' hawkinsi* to be the first representative of irregular echinoids on the basis of its morphological affinities (overall shape and plesiechinid type of compound plating) with pygasteroids (*Plesiechinus*, *Pygaster,* and *Pileus*). However, '*P.' hawkinsi* differs from pygasteroids and other early irregular taxa in three character states: the perforated genital plate 5 (character 5), the absence of supplementary plates (character 9) and a periproct that is not depressed (character 16).

Atlasaster jeanneti Lambert, 1937 is discussed herein because Lambert (1931, 1937) considered this taxon to be an early irregular representative on the basis of what turns out to be an erroneous interpretation of its apical system. *A. jeanneti* possesses none of the apomorphic characters of irregular echinoids, and in the consensus tree, it is placed close to the regular echinoid *D. bowerbankii*, with which it shares smooth primary tubercles (character 31) and the presence of two primary tubercles on interambulacral plates (character 29). More investigations are needed to determine the precise phylogenetic position of *A. jeanneti*, but the present results indicate that it should be considered an early representative of the 'regular' Diadematacea, lacking any phylogenetic affinity with irregular echinoids.

3.b.2. Clade 2

Clade 2 (Fig. 6) is fairly well-supported (decay index ≥ 3) and corresponds to the superorder Eognathostomata as described by Smith (1981), the sister group of all other irregular echinoids ('*P.' hawkinsi* excepted). Apomorphies of the clade are: genital plate 5 reduced or lacking (character 4), exocyclic apical system (character 10), plesiechinid compound plating (character 18), bilaterally symmetric and radially ordered areoles (character 32) and solid primary spines (character 34). As for Clade 1, characters related to specialization of appendages (characters 18 and 32) distinguish the Eognathostomata from other irregular taxa, whereas other character changes (4, 10 and 34) are homoplastic within the Irregularia. The overall morphology of '*P.' hawkinsi* is very close to 'pygasteroid' representatives of the Eognathostomata, as already discussed above. Although *Plesiechinus* can be considered a possible ancestor for the clade, as a representative of basal irregular echinoids,

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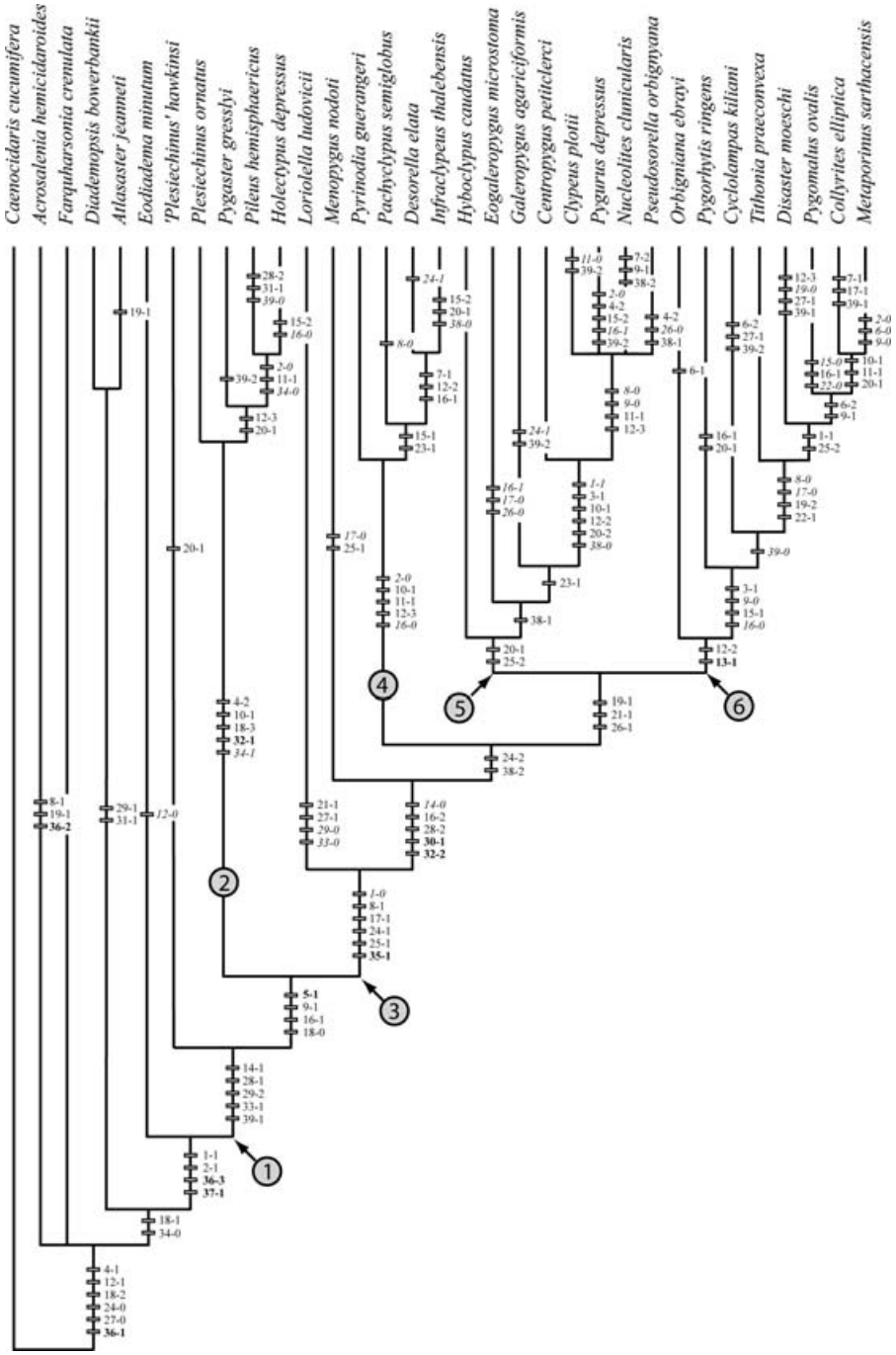


Figure 7. List of character state changes in the majority rule consensus tree. For example: 36-1 = change to state 1 of character 36. Non-homoplastic character changes are in bold; reversals are in italics. Clades discussed in the text are designated by encircled numbers.

it cannot be included in the Eognathostomata because of the plesiomorphic state of the apical system and of the periproct. For the most part, in publications before the 1980s, 'pygasteroid' and 'holectypoid' echinoids were considered completely independent lineages stemming from unrelated 'regular' groups (Durham & Merville, 1957; Melville, 1961; Philip, 1965; Durham, 1966; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Märkel, 1978; Jensen, 1981). In contrast, our analysis supports Smith's view (1981, 1984) and considers 'pygasteroid' and 'holectypoid' echinoids as sister groups in a distinct, monophyletic assemblage. Moreover, our results do not support the traditional dichotomy between 'pygasteroids' and 'holectypoids'. Instead, the taxa *Pileus* (a traditional 'pygasteroid') and *Holectypus* ('holectypoid') form a well-supported clade, excluding the paraphyletic 'pygasteroids' *Plesiechinus* and *Pygaster* (Fig. 6).

3.b.3. *Clade 3*

Clade 3 (Fig. 6) encompasses all irregular echinoids not included in the Eognathostomata and that lack compounded ambulacral plates (reversion to the most plesiomorphic state of character 18), do not possess an Aristotle's lantern as adults (character 35), and do not have a complete and functional perignathic girdle and buccal notches (characters 24 and

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25). This clade corresponds to the superorder Microstomata as described by Smith (1984). Other character changes that distinguish basal Microstomata are highly homoplastic. These are: development of genital plate 2 (character 1), supplementary plates between anterior oculars (character 8), and the depression of ambulacra (character 17).

The basal taxon of the clade is *L. ludovicii,* which is distinguished from other Microstomata by a mosaic of plesiomorphic and apomorphic features (Smith & Anzalone, 2000). Plesiomorphic features that separate it from other taxa in the clade concern the appendages and the periproct. *L. ludovicii* is characterized by a single, large primary spine on each interambulacral plate (characters 29 and 33), ordered primary tubercles with radially symmetric areoles (characters 30 and 32), and a relatively large periproct that is not arranged vertically in a deep anal groove (characters 14 and 16).

Clade 3 differs slightly from the superorder Microstomata as defined by Smith (1984). First, relics of buccal notches and of the perignathic girdle (characters 24 and 25) are present in basal taxa and constitute the apomorphic state for the clade, whereas these structures were considered absent by Smith (1984). Moreover, the present clade includes the 'menopygids' (the genus *Menopygus* and Clade 4) and *L. ludovicii*, taxa not formally included by Smith (1984). This extension of Microstomata agrees with Rose & Olver (1988) and Solovjev & Markov (2004), whereas Smith & Anzalone (2000) consider *L. ludovicii* as the sister taxon of Microstomata.

3.b.4. Clade 4

Clade 4 includes all Microstomata that do not possess specialized ambulacral plates and pores adorally (characters 19 and 21). This description corresponds to the family Menopygidae Lambert & Thiéry, 1911 as it was redescribed by Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966), except for the exclusion of *M. nodoti*. The absence of specialized ambulacral plates and pores adorally distinguishes 'menopygids' from other Microstomata but is not an attribute only of 'menopygids'. For example, Eognathostomata also lack specialized phyllodes, a plesiomorphic character state within the Irregularia. Characters at the base of Clade 4 (characters 2, 10, 11, 12 and 16) are apomorphic character states of the apical system but display numerous homoplastic changes within the Microstomata (Fig. 7). Within Clade 4, some species, such as *Desorella elata* (Desor, 1847) *in* Agassiz & Desor, 1847 and *Pachyclypus semiglobus* (Münster, 1829) *in* Goldfuss, 1826–1844, could be more closely related (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Rose & Olver, 1988), but previous analyses gave too much weight to homoplastic characters of apical structures. Until new material is described, we have no robust argument either to separate *Pyrinodia guerangeri* (Cotteau, 1862) from the other three species or to split the clade formed by these four taxa.

The exclusion of *M. nodoti* from the clade is an essential difference from previous works (Lambert & Thiéry, 1911; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966; Rose & Olver, 1988), especially as the genus *Menopygus* gave its name to the family Menopygidae. *M. nodoti* differs from other 'menopygids' by lack of adoral depression in the ambulacra (character 17), by relics of the perignathic girdle (character 25), and by plesiomorphic character states of the apical system (characters 2, 10, 11, 12 and 16). As discussed above, these characters display important homoplastic changes among the Microstomata.

Rose & Olver (1988) excluded *P. guerangeri* from the Menopygidae and put it in *incertae sedis*, because of the lack of both an intercalary apical system and anal groove. However, *P. semiglobus* exhibits these states as well (a compact apical system and absence of anal groove), even though it is included in the family by the same authors (Rose & Olver, 1988).

3.b.5. Clade 5

Clade 5 comprises Microstomata with compound ambulacral plates adorally and differentiated phyllodes (characters 19 and 21), as well as an anteriorly placed mouth (character 26). However, members of Clade 5 do not have intercalary or disjunct apical systems (characters 12 and 13). In addition, they have differentiated petals (character 20) and no perignathic girdle (character 25), these characters being homoplastic at the level of Irregularia. Clade 5 corresponds to the series Neognathostomata of Smith (1981).

At the base of the Neognathostomata is a paraphyletic assemblage formed by the so-called 'galeropygoids' that includes the genera *Hyboclypus* Agassiz, 1839, *Eogaleropygus* Jesionek-Szymanska, 1978, and *Galeropygus* Cotteau, 1856 (Mortensen, 1948; Kier, 1962; Mintz, 1968; Smith, 1981; Jesionek-Szymanska, 1978). This small paraphyletic group of three taxa partly corresponds to the family Galeropygidae Lambert *in* Lambert & Thiery, 1911 (elevated to the ordinal rank by Mintz (1968)). 'Galeropygoids' constitute the stem group of other Neognathostomata that correspond to the orders Cassiduloida Claus, 1880 *sensu* Mintz (1968), and Clypeasteroida Agassiz, 1872.

Mortensen (1948), Mintz (1968) and Smith (1981) included *Centropygus petitclerci* Lambert, 1901 in the Galeropygidae, whereas it is placed in *incertae sedis* by Kier (1962). This taxon possesses differentiated petals and bourrelets (characters 20 and 23) as well as an exocyclic apical system (character 10). All three of these apomorphic states bring *C. petitclerci* closer to the order Cassiduloida, of which it constitutes the basal taxon, than to the paraphyletic stem group formed by 'galeropygoids'. The order Cassiduloida is supported by numerous synapomorphies, however, it gave rise to the Clypeasteroida in the Palaeogene and is paraphyletic *de facto* (Smith, 1981, 1984; Mooi, 1990; Suter, 1994; Smith, 2001). Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) also included the poorly known species *Jolyclypus jolyi* (Gauthier, 1898) of the Cenomanian within the 'galeropygoids'. However, observation of several newly collected specimens suggests that this species (not included herein) displays close affinities with the genus *Nucleopygus* Agassiz, 1840 from the Upper Cretaceous.

Within the 'cassiduloids', the families Clypeidae Lambert, 1898 (including *C. plotii* and *P. depressus*) and Nucleolitidae Agassiz & Desor, 1847 (*N. clunicularis* and *P. orbignyana*) are not differentiated (Fig. 6). This result agrees with Suter's (1994) phylogenetic analysis of cassiduloids that showed the importance of homoplasies between both families. On the contrary, Kier (1962) differentiated the two families according to petal shape and number of pores in the phyllodes.

3.b.6. Clade 6

Clade 6 includes Microstomata with both a disjunct apical system (character 13) and intercalary apical structure (character 12) and corresponds to the series Atelostomata.

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Although they are considered diagnostic characters of the order Disasteroida Mintz, 1968, characters 12 and 13 undergo reversion in more derived Disasteroida. That is, the apical disjunction is resorbed before the appearance of Cretaceous forms, and compact apical structures appear as early as the Middle Jurassic in *Disaster moeschi* Desor, 1858. What most distinguishes derived Disasteroida from more basal ones (*O. ebrayi*, *P. ringens,* and *C. kiliani*) is the differentiation in size and shape of adoral interambulacral plates (character 22). This differentiation became even more pronounced during the Cretaceous, corresponding to a new phase of diversification that gave rise to the orders Holasteroida Durham & Melville, 1957 (*sensu* Smith, 1981) and Spatangoida Claus, 1876. The differentiation of interambulacral plates is a synapomorphy shared by the three orders Disasteroida, Holasteroida and Spatangoida which constitute the Atelostomata (Devriès, 1960; Fischer, 1966; Mintz, 1968; Kier, 1974; Smith, 1981).

Disasteroida have been subdivided into different families or subfamilies, depending on configuration of apical structures and degree to which the peristome and ambulacra can be depressed (Beurlen, 1934; Jesionek-Szymanska, 1963; Mintz, 1968; Solovjev, 1971; Smith, 1984). However, most of these different taxonomic subdivisions have not been supported by cladistic analyses and seem to constitute paraphyletic grades (however, see Barras (in press) concerning the family Tithoniidae). In the present analysis, three different families can be identified, namely the Tithoniidae Mintz, 1968 (*Tithonia* Pomel, 1883 and *Metaporinus* Agassiz, 1844), Collyritidae d'Orbigny, 1853 (*Collyrites* and *Pygomalus* Pomel, 1883) and Pygorhytidae Lambert, 1909 (*Orbigniana* Ebray, 1860, *Pygorhytis* Pomel, 1883 and *Cyclolampas* Pomel, 1883), all of which constitute paraphyletic groupings.

3.c. Homoplasy levels for key features

Parsimony indices for each character show that values differ considerably according to the character set analysed. Accordingly, characters coding for plate structures of apical systems show high homoplasy values. In particular, the appearance of supplementary plates (characters 6, 7, 8 and 9) and the relationships between the periproct and the posterior plates of the apical system (characters 2 and 11) have the highest levels of homoplasy. Only two characters show low levels of homoplasy and depart significantly from patterns shown by other characters of the apical disc: the loss of perforation in genital 5 (character 5), an apomorphy of all irregulars except '*P.' hawkinsi*, and the disjunction between bivium and trivium (character 13), an apomorphy of the Atelostomata. Most characters describing the density and the organization of tubercles (characters 28, 29, 30 and 32) as well as spine size (character 33) also show low homoplasy values. Highest values are obtained in characters coding for the Aristotle's lantern (characters 35, 36 and 37). Remaining characters show high values of homoplasy; they describe the shape and the position of periproct, the peristome, plate and pore structure of ambulacra and interambulacra, and the overall shape of the test.

3.d. Completeness of the fossil record and stratigraphic congruence

The congruence with stratigraphic range data is sometimes regarded as an additional test of phylogenetic inferences (Wagner, 2000; Benton, Wills & Hitchin, 2000; Pol, Norell & Sidall, 2004). We do not consider stratigraphy as a test of topology in the same way that character distributions are, because the nature of the evidence is totally different. However, we believe that detection of stratigraphic incongruence might point to the need for additional investigations (examination of new fossils and reanalysis of characters). Among the three indices calculated, Relative Completeness Index (RCI) = 13.73, Stratigraphic Consistency Index (SCI) = 0.61, Gap Excess Ratio (GER) = 0.80 (the tested values were significantly different from a random distribution with 0.1 % uncertainty), only the Gap Excess Ratio (GER) value falls within the range of values calculated for echinoids in previous analyses (Benton, Hitchin & Wills, 1999; Villier *et al.* 2004).

Comparisons between raw values of analyses on different taxonomic groups are to be considered cautiously (Pol, Norell & Sidall, 2004), however, it is noticeable that only the Gap Excess Ratio (GER) values obtained in our analysis correspond to values obtained in other works (Benton, Hitchin & Wills, 1999; Villier *et al.* 2004). An explanation may come from the fact that we have selected some taxa of the Lower Jurassic, where the fossil record of echinoids is particularly uneven (Thierry *et al.* 1997; Smith & Anzalone, 2000) and ghost ranges are potentially significant for primitive irregular echinoids. Consequently, low values obtained for the Relative Completeness Index (RCI) are not surprising. On the contrary, the Gap Excess Ratio (GER), that is, the proportion of the total ghost range imposed by the contraints of the cladogram, is not necessarily affected by significant ghost ranges (Wills, 1998). Moreover, the Stratigraphic Consistency Index (SCI) values have been shown to be more sensitive to tree topology than Gap Excess Ratio (GER) values (Benton, Hitchin & Wills, 1999; Wagner, 1995; Pol, Norell & Sidall, 2004), and the majority-rule consensus tree (Fig. 6) shows a pectinate topology with basal taxa characterized by stratigraphic ranges not drastically older than the ranges of terminal taxa.

Our choice of representative species implies the existence of numerous gaps and conflicts between the tree topology and the stratigraphy, as the stratigraphic range of the species selected as representative of a certain combination of characters does not always correspond to the origination date of the clades (most of the irregular clades are supposed to have originated during the Early Jurassic but are poorly known before the Bajocian). For example, *M. nodoti* (Bathonian) is a basal taxon of Microstomata, although more derived species like *E. microstoma* (Middle Toarcian) have an earlier known stratigraphic

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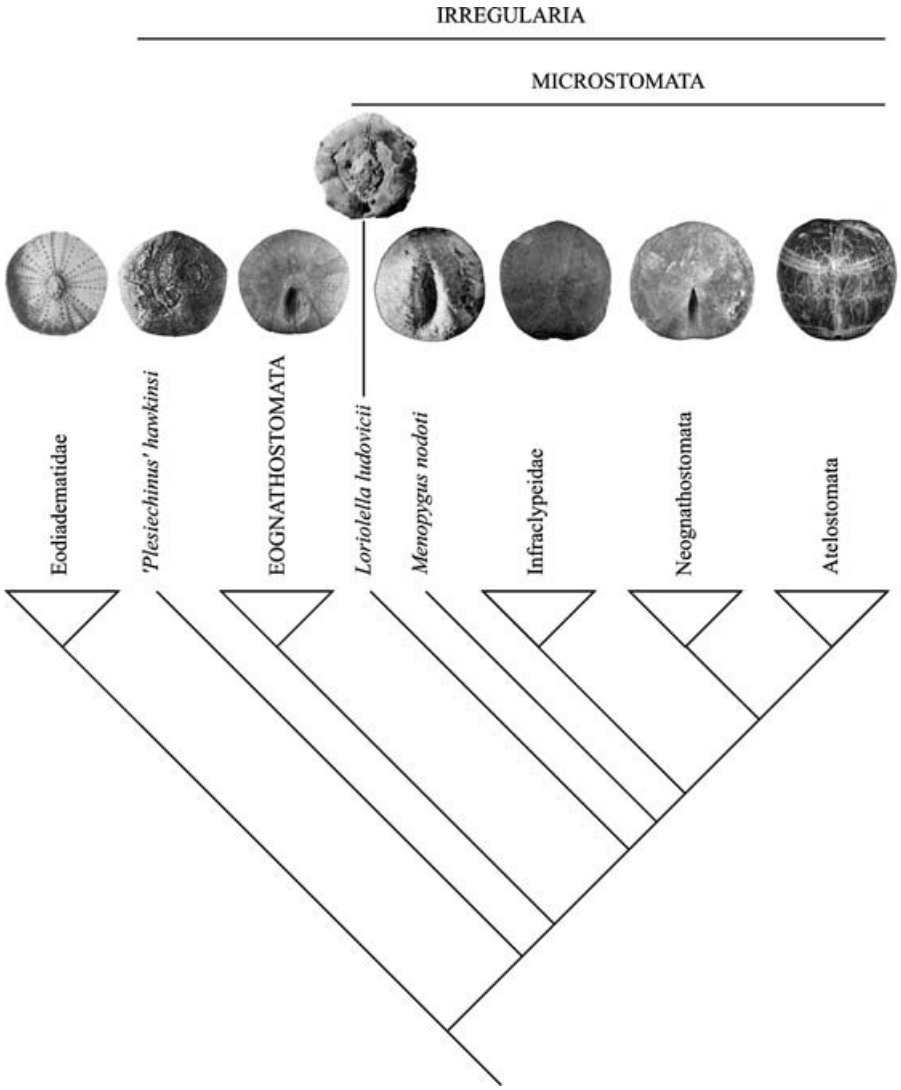


Figure 8. Synthetic representation of the majority rule consensus tree, showing the five main clades of Irregularia. Picture captions from left to right: *Eodiadema minutum*, from Wright, 1855–1860; *'Plesiechinus' hawkinsi,* from Jesionek-Szymanska, 1970; *Pygaster gresslyi*, Votat private collection; *Loriolella ludovicii*, from Smith & Anzalone, 2000; *Menopygus nodoti*, from Rose & Olver, 1988; *Infraclypeus thalebensis*, Clavel private collection; *Centropygus petitclerci*, Claude Bernard University; *Pygomalus analis*, from B. Martin-Garin, unpub. M.Sc. thesis, Univ. Dijon, 2000.

origination. Another example is the basal taxon of Neognathostomata*, Hyboclypus caudatus* Wright, 1851 (Bajocian–Bathonian), which is younger than more derived Neognathostomata such as *G. agariciformis* (Upper Toarcian–Bathonian) or *C. petitclerci* (Upper Aalenian).

4. Taxonomic implications

The present phylogenetic analysis corroborates the monophyly of the Irregularia as well as the other higher taxonomic groupings established by Smith (1984), namely the superorders Eognathostomata and Microstomata, and the series Neognathostomata and Atelostomata (Fig. 8). The analysis also supports the paraphyly of the family 'Galeropygidae' already suspected by previous authors (Kier, 1962; Mintz, 1968). Unlike those of previous workers (Durham & Melville, 1957; Melville, 1961; Fell, 1966), our results suggest the paraphyly of the order 'Pygasteroida'. We also consider the family Menopygidae as a paraphyletic grouping (as opposed to the classifications of Lambert & Thiéry (1911), Mintz (L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966) and Rose & Olver (1988)). All these changes have implications for the way in which we classify sea urchins. We have chosen herein to make reference to PhyloCode principles in the designation of taxa (De Queiroz & Gauthier, 1990, 1992, 1994, among many others), and to rely on stem-based diagnoses of the form, 'the most inclusive clade containing one or more component taxa but excluding others'. PhyloCode designations are restricted to the six main clades discussed above, all being retained in the strict consensus of the 156

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trees. The PhyloCode is designed so that it can be used concurrently with the rank-based codes (Cantino & De Queiroz, 2004), and PhyloCode designations do not invalidate publication criteria as presently established for traditional systematics. As the PhyloCode has not gained universal acceptance for the time being, we have decided herein to give traditional taxonomic designations as well.

PhyloCode designation:
Irregularia [P] Latreille, 1825 (converted clade name)

Diagnosis. The largest monophyletic group containing '*P.' hawkinsi* Jesionek-Szymanska, 1970 but excluding *E. minutum* (Buckman, 1845) *in* Strickland & Buckman, 1845.

Traditional taxonomic designation:
Cohort Irregularia Latreille, 1825 *sensu* Smith, 1981
Remarks. Smith (1984) included *E. minutum* in a new family, the Eodiadematidae, which he considered the first representative of the Irregularia. Members of the Eodiadematidae possess the diamond-shaped teeth of Irregularia, but do not share the other synapomorphies of the clade (that is, the relatively large size of the periproct and the specialization in size and number of spines). We restrict herein the usage of Irregularia to preserve traditional usage, and to hone the description of the group to include those forms that have numerous miniaturized spines and a relatively large periproct. However, we recognize the close affinity between Eodiadematidae and Irregularia. Eodiadematidae certainly constitute the stem group of Irregularia, but are not considered as their first representatives (Fig. 8). Therefore, we do not include *E. minutum* and the family Eodiadematidae within the Irregularia. A consequence of the origin of the Irregularia from a common ancestor with the Eodiadematidae is that 'regular' echinoids do not form a natural grouping, but a paraphyletic stem group for Irregularia. The common term 'regular' remains convenient to designate non-irregular echinoids, but as a taxonomic concept, it is bankrupt.

The basal and oldest known representative of the Irregularia is '*P.' hawkinsi*. This species already has the specialized spines and an overall morphology close to the Eognathostomata and to the species arranged under the generic names *Plesiechinus* and *Pygaster*. '*P.' hawkinsi* is plesiomorphic for characters that concern phyllodes and the structure of the apical system. In contrast, the second oldest known irregular species, *L. ludovicii*, displays large interambulacral spines but specialized phyllodes and a more derived apical structure than '*P.' hawkinsi*. This suggests that the very first irregulars, which radiated during the Early Jurassic, should display a mosaic of plesiomorphic and apomorphic features. As demonstrated by Smith (1978*b*) and Smith & Anzalone (2000), this mosaic depends on the relative degree of specialization of first irregulars for both deposit feeding (*L. ludovicii*) and an infaunal life-style ('*P.' hawkinsi*).

Contrary to Lambert's description (1931, 1937), *A. jeanneti* possesses no synapomorphies with the Irregularia and nothing to justify maintaining it within that clade.

PhyloCode designation:
Eognathostomata [P] Smith, 1981 (converted clade name)

Diagnosis. The largest monophyletic group containing *P. ornatus* (Buckman, 1845) *in* Strickland & Buckman, 1845, but excluding *L. ludovicii* (Meneghini, 1867).

Traditional taxonomic designation:
Superorder Eognathostomata Smith, 1981

Remarks. Because '*P.' hawkinsi* is the basal taxon of the Irregularia, the genus *Plesiechinus* is *de facto* paraphyletic. Consequently, the order Pygasteroida justified by Durham & Melville (1957) and Melville (1961), and including the genera *Plesiechinus*, *Pygaster,* and *Pileus*, is also paraphyletic. Moreover, the clade formed by *P. gresslyi*, *Pileus hemisphaericus* and *Holectypus depressus* (Leske, 1778) makes Pygasteroida paraphyletic as well. However, a more detailed analysis at a lower taxonomic level is needed to determine the precise position of the species within the genera *Plesiechinus*, *Pygaster* and *Pileus*. Concerning 'pygasteroid-like' species, this could lead to the partial abandonment of the generic name *Plesiechinus* in favor of the name *Pygaster*. In this case, the name *Plesiechinus* would be maintained only for the species '*P.' hawkinsi,* as already suggested by Smith (http://www.nhm.ac.uk/palaeontology/echinoids/).

PhyloCode designation:
Microstomata [P] Smith, 1984 (converted clade name)

Diagnosis. The largest monophyletic group containing *L. ludovicii* (Meneghini, 1867) but excluding *P. ornatus* (Buckman *in* Strickland & Buckman, 1845).

Traditional taxonomic designation:
Superorder Microstomata Smith, 1984

Remarks. We include *L. ludovicii* in the Microstomata, of which it represents the earliest form. *M. nodoti* and the clade formed by other menopygids are included in the Microstomata as well, and form a paraphyletic basal grouping. The crowngroup of the Microstomata is subdivided into two sister groups formed by the Neognathostomata and the Atelostomata (Fig. 8).

PhyloCode designation:
Infraclypeidae [P] (new clade name)

Diagnosis. The largest monophyletic group containing both *Infraclypeus thalebensis* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891 and *P. guerangeri*

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(Cotteau, 1862) but excluding *H. caudatus* Wright, 1851.

Traditional taxonomic designation:
Family Infraclypeidae, new family

Type genus: *Infraclypeus* Gauthier, 1875 *in* Cotteau, Péron & Gauthier, 1873–1891

Other genera included: *Pyrinodia* Pomel, 1883, *Desorella* Cotteau, 1855 and *Pachyclypus* Desor, 1858

Diagnosis. Microstomata with an exocyclic apical system and that do not possess specialized ambulacral plates and pores adorally, that is to say, without differentiated phyllodes.

Remarks. The former Menopygidae here constitutes a paraphyletic grouping, and its diagnosis must be changed. *Menopygus* displays a more derived tuberculation and apical structure than *Loriolella*, but does not have synapomorphies with other 'menopygids'. In the present analysis, four menopygids form a clade supported by homoplastic characters, but excluding *M. nodoti* (Fig. 8). As *Menopygus* was the type genus of the former family Menopygidae, we are forced to provide a new name for the 'menopygids' of Clade 4. We propose the most derived genus of the clade, and its type species *I. thalebensis*, as the source for that name, and call the new clade the Infraclypeidae [P].

PhyloCode designation:
Neognathostomata [P] Smith, 1981 (converted clade name)

Diagnosis. The largest monophyletic group containing *H. caudatus* Wright, 1851 but excluding *O. ebrayi* (Cotteau, 1874) *in* Gotteau, Péron & Gauthier, 1873–1891.

Traditional taxonomic designation:
Series Neognathostomata Smith, 1981

Remarks. The Galeropygidae is a paraphyletic grouping and constitutes the stem group of Cassiduloida. 'Galeropygoids' share the plesiomorphic character states of Neognathostomata, such as the absence of bourrelets, and differ fundamentally from basal Atelostomata only by a non-disjunct apical system. In particular, the species *H. caudatus* and *O. ebrayi* (a basal atelostomate) are very similar except for the disjunction of the apical system. This close affinity between certain basal Neognathostomata and basal Atelostomata explains why both clades are more weakly supported (Bremer support = 1, Fig. 6) than the other clades defined herein (Fig. 8). However, basal Neognathostomata and basal Atelostomata are distinguished by a non-homoplastic, unequivocal character dealing with apical structure (disjunction of the apical system) and no confusion is possible. Therefore, phylocode designations are proposed herein for the monophyletic groups Atelostomata and Neognathostomata.

PhyloCode designation:
Atelostomata [P] Zittel, 1879 (converted clade name)

Diagnosis. The largest monophyletic group containing *O. ebrayi* (Cotteau, 1874) *in* Gotteau, Péron & Gauthier, 1873–1891, but excluding *H. caudatus* Wright, 1851.

Traditional taxonomic designation:
Series Atelostomata Zittel, 1879 *sensu* Smith, 1981

Remarks. The Disasteroida is the only representative of the Atelostomata in the Jurassic. It constitutes the stem group of Holasteroida and Spatangoida, which necessarily makes the Disasteroida in the original sense paraphyletic. Within the 'disasteroids', our results do not support the monophyly of Pygorhytidae, Collyritidae and Tithoniidae.

5. Discussion

5.a. Exocyclism and irregularity

Results of our analysis reinforce Smith's conclusions (1981, 1984) concerning the monophyly of Irregularia and the phylogenetic interrelationships existing between the main groups of irregular echinoids (Fig. 8). Moreover, our results permit better assessment and placement of the evolutionary events at the origins of the principal subsets of irregular echinoids, particularly concerning the evolution of apical structures. Therefore, it can be established from the eccentric position of the periproct within the apical circle that the migration of the periproct out of the apical system started at the outset of the origins of the group (in '*P.' hawkinsi*). However, the complete separation between the periproct and the rest of the apical system (= true exocyclism) occurred several times independently, at different times, following different morphological patterns within the different irregular clades as early as the Early Jurassic (in Eognathostomata) and as late as the Late Jurassic (in Microstomata). Therefore, irregularity and exocyclism are not perfectly synonymous terms (Jesionek-Szymanska, 1959; L. W. Mintz, unpub. Ph.D. thesis, Univ. California Berkeley, 1966), and true exocyclism cannot be considered an apomorphy of Irregularia to the exclusion of all 'regular' endocyclic echinoids. Irregularity must be defined by characters of the corona as well, namely the high density and small size of tubercles and spines, and not only by characters of the apical system. The appearance of irregularity is a unique event, accompanied by changes in both the corona and the apical system, whereas exocyclism has occurred independently along several lineages, and does not serve to characterize any single clade. This interpretation relies explicitly on the distribution of evolutionary events in a phylogeny, using several features to support each node instead of relying on the more

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classical idea of using a single, sometimes superficial feature to describe a large and complex taxonomic assemblage.

5.b. Adaptation and homoplasy

The evolution of the first irregular echinoids was achieved through important morphological changes concerning both external and internal features and plate architecture. The external features concerned were spines, tubercles, ambulacral pores (phyllodes and petals) and the periproct, and internal features include the Aristotle's lantern. These features are related to the biological functions of locomotion, nutrition and breathing, and their evolution is controlled by phylogenetic constraints. Adaptive characters are sometimes associated with high levels of homoplasy in irregular echinoids (Suter, 1994; Villier *et al.* 2004). However, our results would show that most of these 'adaptive' characters provide an excellent phylogenetic signal when they are not coded as superficial similarities, but as features that are analysed with phylogenetic definitions of homology firmly in mind. Specialization of the Aristotle's lantern, spines, tubercles and phyllodes constitute apomorphies for the different taxa, and even for the entire Irregularia. The phylogenetic signal yielded by these characters stresses the importance of the environmental context of the origin and diversification of irregular echinoids. The palaeoenvironmental context of the appearance of irregular echinoids is the colonization of new habitats that forced a rapid diversification of the group during the Early Jurassic (Kier, 1974, 1982; Smith, 1978*b*, 1984). Smith (1981) interpreted the reduction in size and the increase in number of spines and tubercles as an adaptation of the first irregular echinoids to locomotion in soft bottom environments and to an infaunal life-style (Smith, 1984). According to Rose & Olver (1984), this is a first step in the specialization of irregular echinoids, and it allows determination of a morphological and stratigraphic boundary between regularity and irregularity.

Smith & Anzalone (2000) showed that the first known Microstomata, *L. ludovicii*, retained large primary interambulacral tubercles and spines. This constitutes evidence of an epifaunal life-style. However, *L. ludovicii* had already adopted a deposit-feeding habit (small peristome, atrophy of the Aristotle's lantern and specialization of ambulacral pores adorally). In contrast, the Eognathostomata retained the lantern to collect the organic component of particles at the surface of the sediment in spite of the fact that they could have lived buried in the sediment (Smith, 1978*b*, 1984). Therefore, in Microstomata, it seems that there has been a rapid and early specialization to deposit-feeding before the appearance of an infaunal or semi-infaunal behaviour. As early as the end of the Liassic, the Microstomata (e.g. *Galeropygus*) possessed specialized tubercles (with asymmetric areoles), a bilateral symmetry of the test, and prominent phyllodes. These characters are adaptations for burrowing (Kier, 1974; Smith, 1978*b*, 1984) and show that at that time, unlike the Eognathostomata, the Microstomata no longer lived semi-epifaunally. Therefore, the two main clades of the Irregularia, the Eognathostomata and the Microstomata, adopted two different strategies in the adaptation to new ecological niches. This explains why adaptative characters are phylogenetically informative in separating the clades.

Periproct migration has an adaptative significance as well. It has been constrained, initiated or fostered by environmental factors (Smith, 1984). However, it accompanies disruptions of apical structures that are developmentally (David, 1990) or epigenetically controlled. This is true only for (1) the whole clade of the Irregularia, characterized by a stretching of posterior oculars and genital 5 in basal taxa, and for (2) basal Atelostomata, distinguished by the disjunction of the apical system into a bivium and a trivium. However, all other characters showed numerous homoplastic changes and illustrate an iterative evolutionary scheme within main irregular clades. For example, vertical orientation of the periproct occurred five times, and the appearance of supplementary plates, the disappearance (atrophy) of genital 5 and exocyclism was realized independently in almost all of the main clades. Unlike Suter's work (1994) on Cassiduloida, this high level of homoplasy cannot be directly interpreted as a result of adaptation to the external environment. This instead suggests invocation of a 'structuralist' explanation, namely internal constraints that limit the disparity of apical structures, as advocated by Rieppel (1989). These constraints may derive from the conservative morphogenetic processes and hierarchical structure of ontogenetic processes (Rieppel, 1989), that is, epigenesis. To sum up, the evolution of the first irregular echinoids (evolution of plate, lantern and appendage features) illustrates the interplay between functionalist (external) and structuralist (internal) factors (Wake, 1989).

5.c. The Extraxial–Axial Theory

The reduction of extraxial body wall and the correlated increase in axial body wall is a general pattern in echinoderm evolution, and particularly in echinoids in which the extraxial region is extremely reduced (David & Mooi, 1996, 1998). In irregular echinoids, the restructuring of the extraxial region (periproct and genital plates), delimited by the axial corona, is realized through a secondary and temporary development of the extraxial part of the body wall within the apical system. It is realized either by the significant increase in periproct size in the Eognathostomata and early Microstomata such as *L. ludovicii* (Smith & Anzalone, 2000), or by the pronounced development

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of supplementary plates in the Microstomata. However, once the periproct has moved down interambulacrum 5 and becomes separated from the apical system, the extraxial component is again reduced. Therefore, the evolution of the apical system of the first irregular echinoids is realized through a temporary (Early and Middle Jurassic) change in the ratio between the extraxial and the axial components of the body wall. This is yet another example of the fact that the interaction of the two major components of the body wall of echinoderms plays an integral role even in those forms in which the extraxial component is the most reduced: the echinoids.

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