PHYLOGENY OF EARLY CRETACEOUS SPATANGOIDS (ECHINODERMATA: ECHINOIDEA) AND TAXONOMIC IMPLICATIONS

by LOÏC VILLIER, DIDIER NÉRAUDEAU, BERNARD CLAVEL, CHRISTIAN NEUMANN *and* BRUNO DAVID

ABSTRACT. A phylogenetic analysis of 36 species provides a test for the taxonomy and the history of Early Cretaceous spatangoids. Most taxonomic units from genera to suborders are consistent with the proposed phylogenetic framework. We retain Hemiasterina, Micrasterina, Hemiasteridae, Schizasteridae, *Hemiaster*, *Heteraster*, *Mecaster*, and *Periaster* as original monophyletic groups. However, all of these clades originate without the classical apomorphies normally ascribed to them. We suggest a revision of their diagnoses and of the generic attributions of basal species. Some ill-defined, 'primitive', and paraphyletic taxa are recognised: *Toxaster*, *Epiaster*, *Palhemiaster*, and Toxasteridae. Even if they do not have phylogenetic meaning, they are retained here, pending a more complete revision.

KEY WORDS: Spatangoida, Echinoidea, phylogeny, systematics, Cretaceous.

THE phylogeny of higher-level taxa of echinoids (order and above) is now considered to be robust (Smith 1981, 1984). In this framework, the order Spatangoida appears as a well-supported monophyletic group, with its first occurrence in the lowermost Cretaceous (Berriasian). While the monophyly of Spatangoida is largely consensual, the precise origin of the order is still unclear and has been the subject of several hypotheses in the last 50 years. Eble (2000) noted the lack of phylogenetic information for early Spatangoida and Holasteroida. Roots of these two orders are generally sought in disasteroid-like ancestors. Beurlen (1934) and Mortensen (1950) proposed *Metaporinus* as the ancestor of the Spatangoida. However, this hypothesis implied a reversion to a compact structure of the apical system because the first Disasteroida had already evolved by extension and disjunction of the apical system. Durham and Melville (1957) rooted the Spatangoida within the Galeropygidae. Their alternative hypothesis excluded the reversion but implied a stratigraphical gap of more than 50 myr. Later, Durham (1966) suggested that the Holasteroida, Spatangoida and Cassiduloida arose from a common ancestor at the beginning of the Jurassic. Afterwards, most authors retained the hypothesis of Devriès (1960a) that holasteroids and spatangoids both arose from disasteroids (Fischer 1966; Mintz 1966; Smith 1981, 1984). According to Devriès (1960a) the first spatangoid is *Toxaster laffittei* from the Berriasian. This species displays transitional features between Disasteroida and Spatangoida, such as a compact apical system and protamphisternous plastron. Other transitional forms to the more derived Spatangoida are found in nominal species such as *Toxaster holasteroides* and *T. africanus*, that show a progressive compaction of the apical system to an ethmophract pattern. However, consensus is still lacking. For example, Clavel (*in* Jablonski and Bottjer 1990) rejected *Toxaster laffittei* as a Spatangoida and moved it to Holasteroida as *Holaster cordatus*. In this latter hypothesis, *Proholaster auberti* is a good candidate for ancestor of the Spatangoida.

Smith (1984) proposed an evolutionary tree at the family level (Text-fig. 1A). Toxasteridae appeared first from a disasteroid ancestor. From the Berriasian to the Aptian, diversification gave rise to three genera of the family Toxasteridae (*Toxaster*, *Aphelaster*, and *Heteraster*). These genera (especially *Toxaster*) operated as a rootstock for all later Spatangoida. The suborders Hemiasterina and Micrasterina evolved successively from two different toxasterid ancestors by acquisition of a peripetalous and a sub-anal fasciole, respectively. Each suborder was represented by a single family (Hemiasteridae and
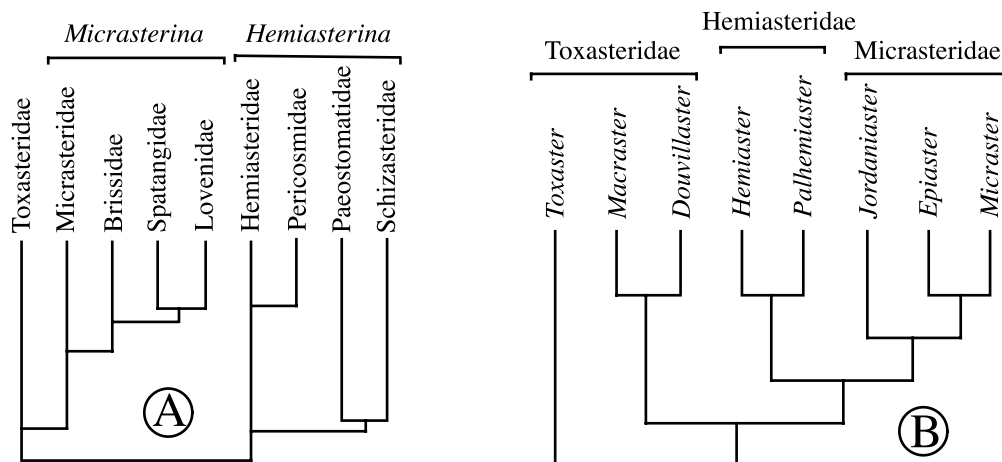
TEXT-FIG. 1. Current phylogenetic schemes for spatangoid relationships. A, evolutionary tree proposed for spatangoid families (Smith 1984). This tree synthesises data in older works such as Beurlen (1934), Mortensen (1950), Fischer (1966), Mintz (1968), and Smith (1981). B, the most recently published phylogeny of early spatangoids (Neumann 1999).

Micrasteridae) during the Early Cretaceous, and started to diversify from the Early Cenomanian when the Hemiasteridae gave rise to the sister clades Palaeostomatidae and Schizasteridae, and from the Santonian when the Brissidae originated from the Micrasteridae.

First treated as 'natural entities', the validity and status of some families and genera have been recently discussed. Néraudeau and Floquet (1991) and Néraudeau (1994*a*) suspected that the family Hemiasteridae was diphyletic. Then Néraudeau (1994*b*) formally excluded *Palhemiaster* and *Mecaster* from the hemiasterids and put these two genera in a different, *incertae sedis* family. Neumann (1999) proposed a phylogeny of Early Cretaceous and Cenomanian spatangoids (Text-fig. 1B). Three large monophyletic groupings were recognised: the taxa Hemiasterina and Micrasterina and a new clade made of *Douvillaster* and *Macraster*. The Toxasteridae appears as a paraphyletic set with *Toxaster* at the base of the tree.

This historical summary suggests that most taxa are stable, and quite well defined. However, their phylogenetic relationships remain unclear and the validity of early spatangoid taxa requires further testing in a phylogenetic framework. We conduct herein a phylogenetic analysis at the species level for the earliest Spatangoida (Early Cretaceous and Early Cenomanian genera). Monophyly of the order Spatangoida will be taken for granted (see Jensen 1988) and relationships with the related orders Holasteroida and Disasteroida will not be discussed. We have three main objectives: (1) to provide a phylogeny for the early radiation of the Spatangoida; (2) to delineate the meaning of genera and families in a phylogenetic framework; and (3) to attempt a taxonomic revision based on the inferred phylogeny.

MATERIAL AND METHODS

Selection of taxa

Because the Spatangoida comprises hundreds of species, it would not be realistic to undertake a taxonomic and phylogenetic revision of the order at the species level. In this paper, we intend to describe the initial radiation of the order, but not to consider all of its subsequent history, which remains confused by evolutionary convergence and reversal in younger taxa (see Fischer 1966; Kier 1974). Thus, our analysis emphasises the phylogeny of the primitive Toxasteridae (*sensu* Fischer 1966) and their relationships with some younger families. We limit the stratigraphic range of the study from the first appearance of indisputable Spatangoida (Berriasian) to the Early Cenomanian, when the first presumed members of the families Micrasteridae and Schizasteridae appeared.

TABLE 1. List of spatangoid genera cited from the Lower Cretaceous and the Cenomanian. The last three genera are not included in the analysis. *Physaster* and *Leiostomaster* were excluded because their occurrence in the Albian–Cenomanian is doubtful, their first unequivocal occurrences being in the Senonian. Considered as a holasteroid in the Treatise on Invertebrate Paleontology, *Physaster* is now a junior synonym of *Homoeaster*, a Late Cretaceous spatangoid (Smith and Jeffery 2000). *Somalechinus* is a very poorly described genus, known from a single species doubtfully dated at Cenomanian. Stratigraphical data modified from Fischer (1966).

Genus	Stratigraphic range
Aphelaster Lambert, 1920	Valanginian
Douvillaster Lambert, 1917	Aptian – Turonian
Epiaster d'Orbigny, 1854	Aptian – Senonian
Hemiaster Desor, 1847	Aptian – Recent
Heteraster d'Orbigny, 1853	Hauterivian – Cenomanian
Macraster Roemer, 1888	Aptian – Cenomanian
Mecaster Pomel, 1883	Cenomanian – Thanetian
Micraster Agassiz, 1836	Cenomanian – Danian
Palhemiaster Lambert, 1916	Aptian – Cenomanian
Periaster d'Orbigny, 1853	Cenomanian – ? Eocene
Polydesmaster Lambert, 1920	Cenomanian
Toxaster Lambert, 1920	Berriasian – Cenomanian
Washitaster Lambert, 1927	Albian – Cenomanian
Leiostomaster Lambert, 1920	? Albian – Senonian
Physaster Pomel, 1883	? Albian – Senonian
Somalechinus Checchia-Rispoli, 1945	Cenomanian

Fifteen genera of Spatangoida appeared during the Early Cretaceous and the Early Cenomanian (Table 1). Following the classification of Fischer (1966), they are distributed within five families: Toxasteridae, Hemiasteridae, Micrasteridae, Palaeostomatidae and Schizasteridae. However, only 12 genera have been retained in our study. Two other nominal genera (*Physaster* and *Leiostomaster*) were excluded because their occurrence in the Albian–Cenomanian is doubtful, their first unequivocal occurrences being in the Senonian. We have also excluded *Somalechinus*, which is a very poorly described genus known by a single species doubtfully dated as Cenomanian (Checchia-Rispoli 1945). Several species were selected in each genus according to three major constraints: (1) the validity of the species had to be incontestable; (2) the selected species had to cover the majority of the stratigraphical range of each genus; and (3) they had to be illustrative of perceived morphological diversity (Appendix).

Disaster elongatus and *Holaster cordatus* have been chosen as outgroups. They root the tree with primitive states of Disasteroida, and Holasteroida, respectively. It is important to note that we used type specimens of '*Toxaster*' *laffittei* as representative of *H. cordatus*. Indeed, although initially described as a toxasterid by Devriès (1960a) '*Toxaster*' *laffittei* is now considered a holasteroid. It was originally placed in the genus *Eoholaster* (Solovjev 1989), and later synonymised with *Holaster cordatus* by Clavel (*in* Jablonski and Bottjer 1990), a position followed by Eble (2000).

Nine *Toxaster* species were used to sample the morphological disparity, and to cover the stratigraphic range of the genus from the Berriasian to the Cenomanian. Our selection was also guided by previous phylogenetic hypotheses considering *Toxaster* species as ancestors of other genera. The nine species are: *T. retusus*, the genotype species; *T. rochi*, as a primitive member of the genus; *T. granosus*, for the Valanginian; *T. maurus*, *T. villei* and *T. peroni*, which are considered as leading to *Palhemiaster*; *T. seynensis* and *T. collegnoi*, supposed to be at the origin of *Hemiaster*; and *T. radula*, as a derived Albian species.

Six species were retained to represent *Heteraster*: *H. corvensis*, as the most primitive member of the genus [this species, like some other species of Portuguese *Heteraster*, was originally classified as a *Toxaster*, but is now considered to be a true *Heteraster* (Rey 1972)]; *H. texanus*, for American species;

*H. subquadratu*s, for its rounded shape; *H. oblongus*, as the type species; and *H. transians*, which was described as an atypical *Heteraster* by Devriès (1956).

Lambert (1926) described *Washitaster* for *Toxaster*-like *Heteraster* with multiple lateral fascioles, but without heterogeneity of the unpaired ambulacra. Despite this quite clear original definition, the genus was not always used in a consistent way. For example, Cooke (1955) considered *Washitaster* as a subgenus of *Heteraster*. Fischer (1966) mentioned *Washitaster* as a valid genus, but attributed it to the Hemiasteridae. Finally Néraudeau (1994*b*) excluded the genus from the family Hemiasteridae and considered it as a toxasterid. According to the variability in the use of this genus, only the type species (*Washitaster riovistae*) has been retained.

The genus *Epiaster* comprises a wide range of shapes. This great disparity has induced some fuzziness in the use of the genus, and its taxonomic value has been repeatedly criticised (Fischer 1966; Lobacheva 1968; Smith 1988). To avoid *a priori* assumptions about the phylogenetic position of *Epiaster*, and to take its variability into account, seven nominal species are included to cover a time span from the Aptian to the Cenomanian. Note that some of these species have previously been classified in other genera.

The three toxasterid genera *Aphelaster*, *Macraster*, and *Douvillaster* are small and poorly studied. We have sampled a few species, with at least the type species of each genus.

The genus *Hemiaster s.l.* is considered to be a diphyletic grouping (Lambert 1931; Néraudeau and Floquet 1991; Néraudeau 1994*a*). One clade originates from *Toxaster collegnoi* and gives rise to *Hemiaster s.s.* and then to *Bolbaster* (Néraudeau 1990, 1994*b*). The second clade leads from *Palhemiaster peroni* to the *Mecaster* radiation (ibid.). These two potential ancestors and some of the oldest species of each clade have been included in our sampling, namely: *Palhemiaster peroni*, *P. comanchei*, *Toxaster collegnoi*, *Hemiaster dalloni*, *H. zululandensis*, and *Mecaster batnensis*.

The origin of the Schizasteridae is not clearly understood, although the family seems to appear within the Hemiasterina by acquisition of a second fasciolar branch (Néraudeau 1994*a*). According to Fischer (1966), *Washitaster*, which displays multiple fasciolar branches, may exhibit features of schizasterids. The oldest schizasterid is the genus *Periaster*, but it is very distinct from all potential ancestors.

Néraudeau (1994*b*) suggested a polyphyletism of the family Schizasteridae with at least one lineage rooted within the genus *Leymeriaster*, leading to *Schizaster*, and another independent lineage with the genus *Periaster* as a basal group. Our study considers only the two older known species of *Periaster* (*P. elatus* and *P. undulatus*) and does not claim to resolve the taxonomic value of the family Schizasteridae (but see discussion below).

From a classical point of view, the family Micrasteridae is derived from a toxasterid ancestor by development of a sub-anal fasciole. Yet Stokes (1977) showed that the expression of this fasciole varies within a species or a genus. The first micrasterids that exhibit a subanal fasciole are Cenomanian species of the genus *Micraster*. However, some species without subanal fascioles and the first named *Epiaster* belong to the order Micrasterina and probably to the genus *Micraster* (Smith 1988; Néraudeau *et al.* 1998; Néraudeau and Mathey 2000). Two species, with and without a fasciole, have been analysed: *Micraster michelini* and *M. distinctus*.

Coding of characters. Cladistic analysis at the species level is uncommon for fossil taxa (Benton *et al.* 1999) and such studies for fossil sea urchins are few (e.g. Smith and Wright 1989, 1990; Jeffery 1999; Mooi *et al.* 2000). Robustness of trees, correlation, and consistency of characters have rarely been tested. Theoretically, this scarcity of cladistic work should invite an agnostic approach in which the maximum number of characters is coded without *a priori* selection and polarisation of states. Nevertheless, papers abound on the evolutionary history of echinoids. Many different approaches have been developed (David 1993) and provide a test for the taxonomic or environmental significance of characters at different taxonomic levels. For example, in Recent and fossil Spatangoida, environmental parameters partly control morphological traits of species (Chesher 1963; Kanazawa 1992; Néraudeau 1995), and can determine heterochronic trends (McNamara 1985; Néraudeau 1991, 1992). Therefore, a reasoned sorting of characters based on test architecture may reduce the bias of environmental influences (David 1988; Mooi and David 1996). For the purpose of this study, a set of 35 characters was coded. Each was polarised

by comparison with the two selected outgroups, *Disaster elongatus* and *Holaster cordatus*. Polymorphism was not coded, but when a species expressed several states, the most frequent was retained.

Computing trees. A data matrix of 35 characters coded for 36 taxa (Appendix) was analysed with the software PAUP 3.1.1 (Swofford 1993). Characters are considered as unordered to avoid *a priori* assumptions about possible morphoclines. The features expressed in the two outgroups (*Disaster elongatus* and *Holaster cordatus*) specify the primitive state for each character. The most parsimonious trees were calculated with the 'Branch and Bound' algorithm (Hendy and Pendy 1982), which provides exact results for a set of 10–30 taxa. The ACCTRAN option, which favours reversions, has been retained. Unresolved parts of the trees are figured as polytomies. When several trees are obtained, a Strict Consensus Tree and a Majority Rule Tree are computed. Two kinds of indices are calculated to describe the resulting trees: classical metrics of parsimony (Consistency Index, Retention Index, and Rescaled Consistency Index) and tests of congruence with stratigraphic data (Stratigraphical Consistency Index, Relative Completeness Index, Gap Excess Ratio). The software PAUP 3.1.1 directly produces parsimony indices but stratigraphical congruence indices are provided by the software GHOSTS 2.4 (see Wills 1999*a*, *b*). Significance of the latter is tested by a permutation test, which involves a comparison of the tree values to the distribution of 500 random permutations. The data matrix includes no basal synapomorphies, and the non-homoplastic autapomorphies have been excluded to prevent artificial inflation of parsimony indices.

CHARACTER ANALYSIS

Tuberculation. The type of spine and its layout on the test are clearly correlated with mode of life (Smith 1980*a*; Kanazawa 1992). However, tuberculation is also largely used to support taxonomic distinctions (Mortensen 1950, 1951). For all the species reviewed, the plastronal area shows great density of disjunct to partially contiguous tubercles. Their size decreases near the posterior part of the test. The size of the tubercles stays quite similar all over the oral face, but the scrobicular area may be enlarged in the anterior interambulacra. On both sides of the plastron, the posterior paired ambulacra are generally smooth or develop a scattered tuberculation in some species, but the variations are not significant enough to justify two character states. The anterior paired ambulacra always show some scattered tubercles. On the aboral side, tubercles of the lateral interambulacra (1 and 4) become smaller and less dense near the apex in the oldest species (Text-fig. 2A). In some more recent species, tubercles become locally denser just beneath the apex. The density of the tubercles can also increase in the anterior interambulacra (2 and 3). This denser and finer tuberculation can also be associated with an enlargement of the scrobicular area (Text-fig. 2D). In addition, on each side of the anterior groove, a narrow strip of very dense, small tubercles occurs in all but the most primitive species (Text-fig. 2C–D).

Three characters with significant variations have been retained for the tuberculation.

1. Density of primary tubercles on the aboral portion of the interambulacra: 0, size and density decreasing from the ambitus to the apex; 1, constant, high density (Text-fig. 2B).
2. Shape of primary tubercles on the aboral portion of the interambulacra: 0, never scrobiculated; 1, a few tubercles scrobiculated.
3. Tuberculation on each side of the anterior groove: 0, same as in the other parts of the anterior interambulacra; 1, strip of dense small primary tubercles.

Fascioles. Fascioles are bands of tiny tubercles bearing small, heavily ciliated, mucus-secreting spines. The classification of spatangoid families is based, to a large extent, on the position and the number of fascioles (Durham and Melville 1957; Fischer 1966). However, fasciole categories, defined by their position on the test, are not always homologous. For example, peripetalous fascioles appear with different ontogenetic sequences in the hemiasterid *Hemiaster expurgitus* and in the schizasterid *Abatus cordatus* (Mortensen 1907; Mespoulhé 1992; Solovjev and Markov 1999; David *et al.* 2000). Moreover, Néraudeau *et al.* (1998) defined different textures in fascioles (i.e. protofascioles, parafascioles and orthofascioles). Protofascioles are made of aggregated but unorganised miliaries. They appear locally at the ends of the petals and more generally in the lower part of the frontal groove (Text-fig. 3A). Parafascioles are defined as
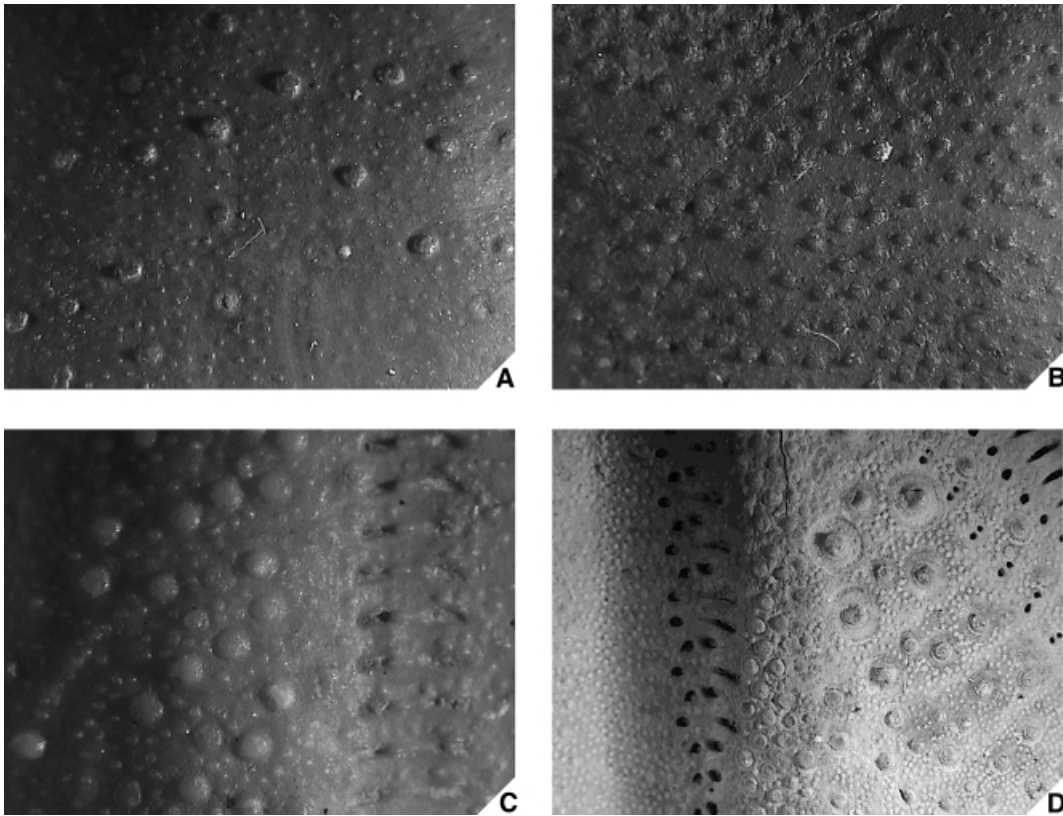
TEXT-FIG. 2. Characters of tuberculation. A, low density of primary tubercles from the lateral side of interambulacrum 1, near the apex of *Heteraster transians*, Djebel Kerker, Algeria, Albian, A. Devriès collection, University of Poitiers; ×9. B, high density of primary tubercles on the lateral side of interambulacrum 1 of *Hemiaster dalloni*, Jugo, Spain, Early Cenomanian, R. Ciry collection, University of Burgundy, GD 2366; ×9. C, homogeneous primary tubercles beside the anterior groove of *Epiaster heberti*, Djebel Chegaig, Algeria, Cenomanian, A. Devriès collection, University of Poitiers; ×17. D, strip of dense, small primary tubercles beside the anterior groove of *Heteraster delgadoi*, Comillas, Spain, Early Albian, Muséum National d'Histoire Naturelle, Paris (MNHN), R.63540; ×6.

alignments of miliaries that could include primary tubercles (Text-fig. 3B). They can occur on the posterior keel or on sides of the test from the ambitus up to the apex. In lateral and peripetalous positions parafascioles show diverse structures, from local discontinuous alignments to a large band with patches having different directions of alignment (Text-fig. 3C). Orthofascioles correspond to the 'classical' fascioles. In orthofascioles, miliaries are dense and arranged in well-defined series without intercalated primary tubercles. Orthofascioles may be multiple and discontinuous, or show transition to parafascioles (Text-fig. 3D). Actually, intermediate states exist between the three textural types. The textural approach to fascioles is necessary to describe primitive fascioles that are abundant but too rarely taken into account in Early Cretaceous spatangoids.

An accurate description of fascioles should consider their position on the test as well as the texture of the tuberculation. However, peripetalous, latero-anal, and marginal fascioles cannot be regarded with certainty as homologous from one group to another. Therefore, those categories cannot be coded according to their usual definitions. Protofascioles are likely to have evolved once, and correspond thus to an apomorphy in spatangoid evolution; on the other hand, orthofascioles appeared through convergence in various lineages (Néraudeau *et al.* 1998). New observations on Early Cretaceous toxasterids suggest that
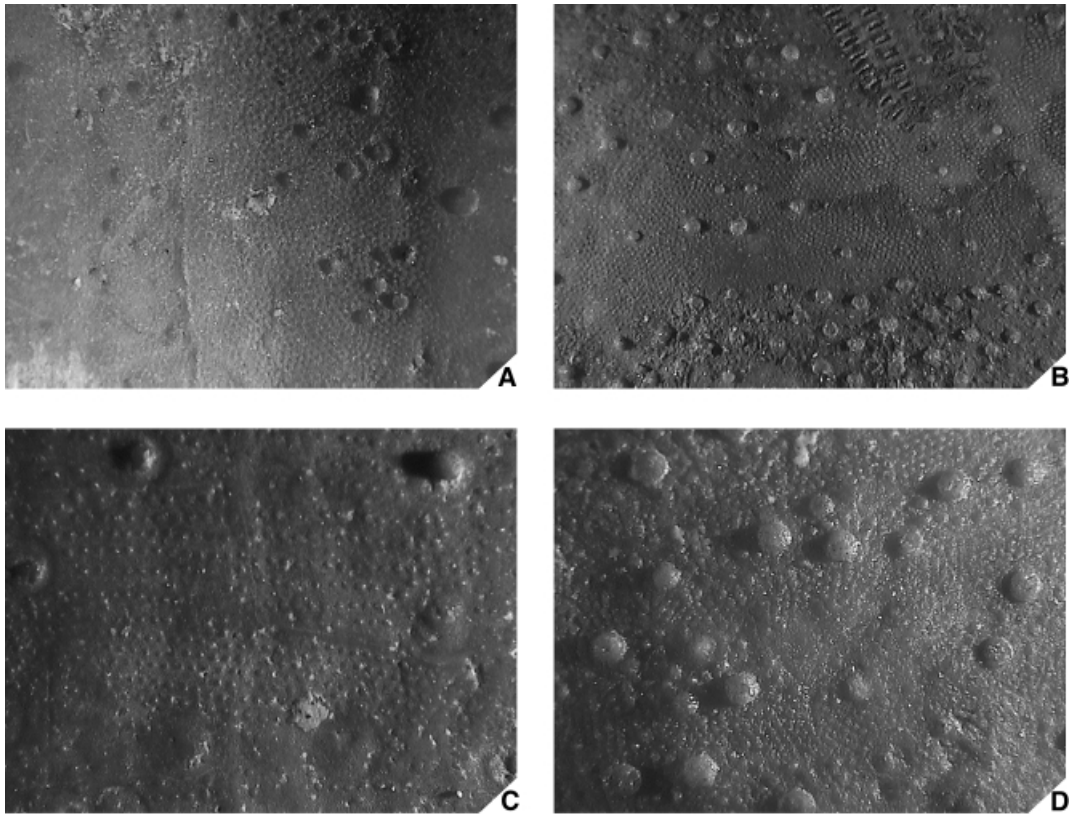
TEXT-FIG. 3. Texture of the fascioles found in primitive spatangoids. A, high density of miliary tubercles defining protofasciolar texture at the extremity of the anterior ambulacrum of *Toxaster collegnoi*, Teruel, Aptian, A. Devriès collection, University of Poitiers; ×12. B, parafasciole corresponding to high concentration of miliary tubercles, including a few primary tubercles, at the extremity of the petal in ambulacrum V of *Hemiaster zululandensis*, Ambarimaninga, Madagascar, Albian, M. Collignon collection, University of Burgundy, GD 2367; ×8. C, parafasciole showing large band of variably aligned miliary tubercles in *Heteraster transians*, Djebel Kerker, Algeria, Albian, A. Devriès collection, University of Poitiers; ×12. D, local strips of orthofasciole in *Washitaster riovistae*, Riovista, Texas, Upper Albian, Lambert collection, MNHN J.07000; ×12.

the appearance of parafascioles may also correspond to a single evolutionary event. Presently, the only way to delineate plausible homologies is to combine position and texture. But coding fascioles will remain tentative until ontogenetic data can enlighten the transition from one structure to another. Consequently, we restrict the coding of fascioles to three characters.

4. Protofascioles at the end of the petal and/or the frontal groove: 0, absent; 1, present.
5. Subanal fasciole: 0, absent; 1, parafasciole or orthofasciole.
6. Peripetal and/or marginal fascioles in the interambulacra 1 and 4: 0, absent; 1, discontinuous parafasciole; 2, a large parafasciole band; 3, parafascioles associated with orthofascioles.

General features of the ambulacra. Devriès (1960*a*) emphasised the importance of ambulacral features to decipher the early evolution of spatangoids, and particularly the emergence of the Toxasteridae. A progressive differentiation of the podia and the ambulacra within Toxasteridae corresponds to a functional specialisation. This evolutionary trend is brought about through ontogenetic changes. Early in ontogeny

the five ambulacra are all identical. They develop by the modification of paired ambulacra which differentiate from ambulacrum III, and next by independent growth of the anterior and posterior pairs. This ontogenetic differentiation of ambulacra is correlated with important adult variation and affects, among other things, pore morphology, shape, and symmetry of the ambulacra (Text-fig. 4). Trends exist independently for frontal, anterior, and posterior paired ambulacra.

The differentiation of an adapical segment of the ambulacra into a petal is classically described by three states: non-petaloid, sub-petaloid, and petaloid, referring mostly to the pattern of the distal end. However, the distal end of the petals is highly variable during ontogeny and amongst taxa. We describe and code the
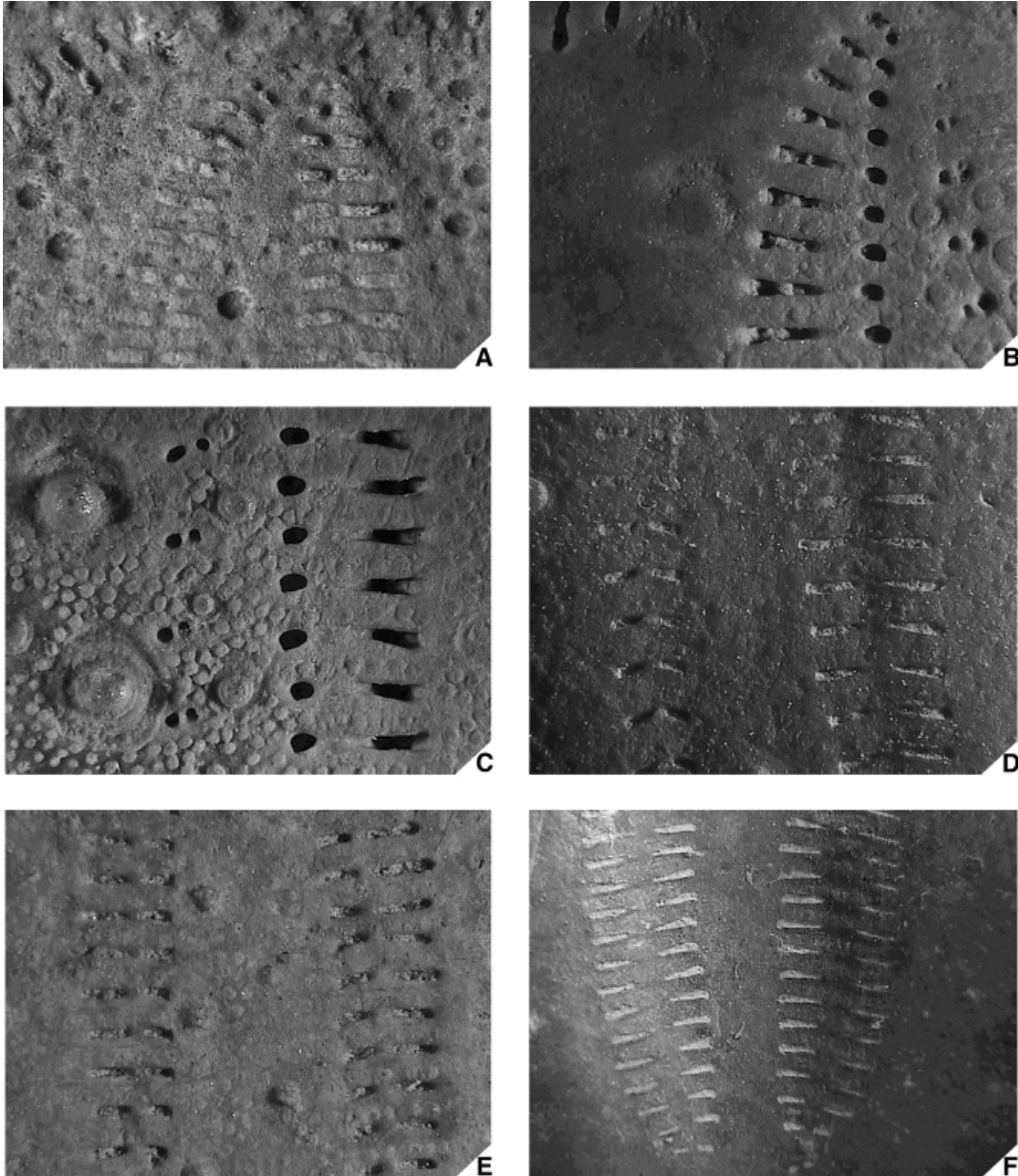
termination of the petals of the early spatangoids from personal observation and separately from the classical scheme. When petals are not fully differentiated (non-petaloid), pore pairs extend from the apex to the peristome along a straight line without conspicuous change in size and shape. The sub-petaloid type involves a progressive differentiation of petal, over several plates (Text-fig. 5A). In 'linear petals', the branches stay straight and parallel but the pores become suddenly shortened. The term 'divergent petals' is proposed herein for petal terminations with a clear reduction of pore length, a progressive rotation of the pore pairs and an S-shape of the anterior branch of the petal (Text-fig. 5B–C). Closed petals correspond to an abrupt change in pore size, shape and orientation (Text-fig. 5D). The frontal ambulacrum does not show such a variety of features and terminations, and displays only two states (sub-petaloid or linear). The general shape of the petals varies from straight to sinuous, but some morphologies are more complex with a straight portion in the distal part of the petal and a weakly sinuous portion near the apical edge. Petals can show a differentiation of pores between their two ambulacral branches (Text-fig. 4B–D). This induces a loss of symmetry during ontogeny. During early ontogeny, the petal is symmetrical. Subsequently, the pores of the posterior branch become larger than the anterior ones, leading to an asymmetrical state (Text-fig. 4A–B). A secondary symmetry may occur next by enlargement of the pores in the anterior branch (Text-fig. 4E–F). In this case, the asymmetrical pattern remains near the apical edge of the petals, where pores are younger.

The relative size of the ambulacra is also used in taxonomy. We coded the relative length of the paired petals (degree of equipetality) following a gap coding method. Equipetality is measured as the ratio between the length of the posterior petal (LI) and the anterior petal (LII) (Néraudeau and Floquet 1991). It indicates the degree of differentiation of petals: nearly equal length of posterior and anterior petals is equipetality, whereas short posterior and long anterior petals are a state of so-called inequipetality. Relative length of petals is expected to be sensitive to environmental variations but also to support phylogenetic information. Indeed, diphyletism of the Hemiasteridae was initially supported by distinction of true *Hemiaster* with relatively short posterior petals and *Mecaster* with anterior and posterior petals of similar length. The distribution of this ratio is trimodal with two gaps that have been used to identify three classes: $LI/LII < 0.55$ means inequipetality, $0.55 < LI/LII > 0.8$ means sub-equipetality and $LI/LII > 0.8$ means equipetality. In the frontal ambulacrum, the length of the petaloid portion varies to a large extent. This has been coded as either 'large', where the petal reaches the ambitus, or 'short' where the petal reaches only to the middle of the ambulacrum, plus an intermediate state.

Ten characters are coded in the matrix to express the differentiation of ambulacra and their general features.

7. Differentiation of the ambulacra: 0, all identical; 1, ambulacrum III differentiated.
8. Symmetry of the anterior paired petals: 0, yes; 1, no; 2, yes but asymmetric near the apex.
9. Symmetry of the posterior pair petals: 0, yes; 1, no; 2, yes but asymmetric near the apex.
10. Termination of paired anterior petals: 0, sub-petaloid; 1, divergent; 2, in linear branches; 3, closed.
11. Termination of paired posterior petals: 0, sub-petaloid; 1, divergent; 2, in linear branches; 3, closed.
12. Frontal ambulacrum: 0, in linear branches; 1, sub-petaloid.


TEXT-FIG. 4. Growth pattern and symmetry of the ambulacra. A, primitive isometric growth pattern of isopores observed on the apical end of ambulacrum I in *Toxaster ricordeaui*, Saint-Dizier, France, Barremian, University of Lyon, EM 10,000; ×16. B, asymmetry of paired ambulacra, resulting from growth pattern of the posterior branch from nearly symmetrical isopores near the apex to highly asymmetrical anisopores in the petals, in ambulacrum II of *Heteraster delgadoi*, Comillas, Spain, Early Albian, MNHN R.63540; ×13. C, highly asymmetrical petals, with a different number of plates in each branch, the anterior branch bearing small isopores and the posterior branch elongate anisopores, in ambulacrum IV of *Heteraster delgadoi*, Comillas, Spain, Early Albian, MNHN R.63540; ×10. D–E, asymmetrical petals, with primitive isopores in the anterior branch and elongate anisopores in the posterior branch. D, *Toxaster seynensis*, Seynes, France, Barremian, B. David collection, University of Burgundy, GD 2368; ×12. E, *Toxaster retusus*, France, Hauterivian, B. David collection, University of Burgundy, GD2369; ×10. F, symmetrical petals displaying large elongate isopores, with a wide interporal partition, in ambulacrum V of *Epiaster restrictus*, Bordj Oultem, Algeria, Late Aptian, A. Devriès collection, University of Poitiers; ×9.
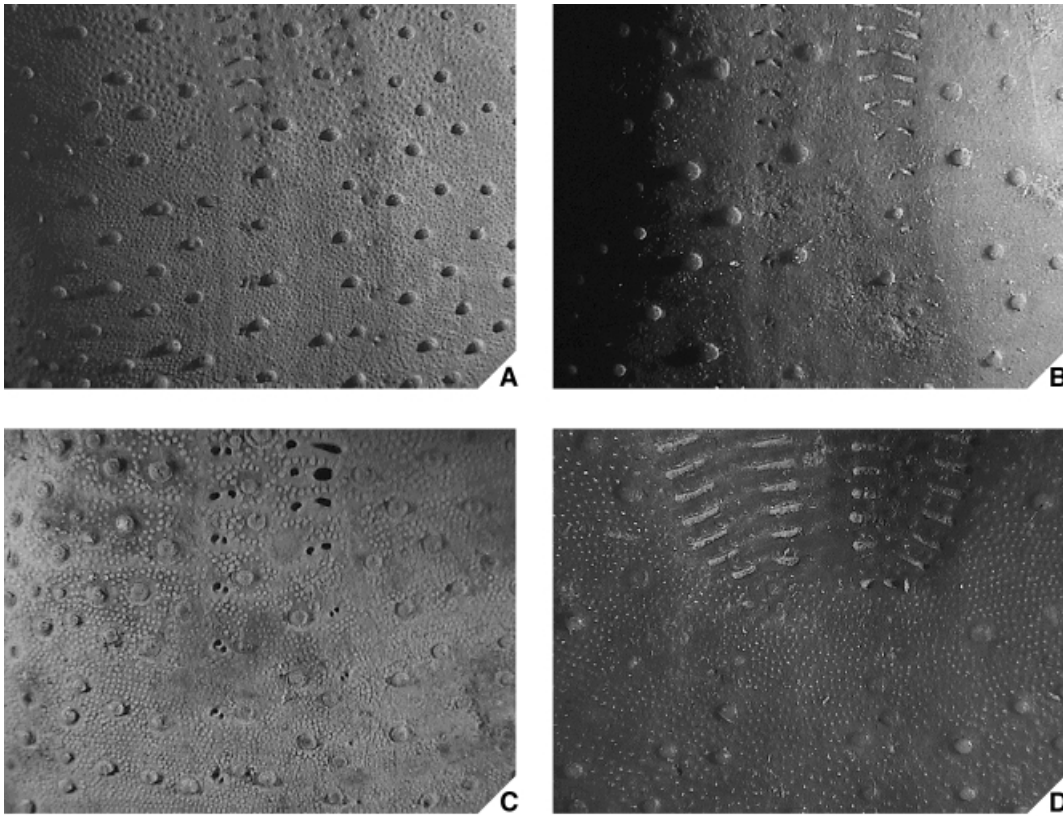
TEXT-FIG. 5. Termination of the paired petals. A, sub-petaloid termination: *Toxaster ricordeaui*, Saint-Dizier, France, Barremian, University of Lyon, EM 10,000; ×6. B–C, termination by constriction of the ambulacral branches and divergent distal parts. B, *Toxaster seynensis*, Seynes, France, Barremian, B. David collection, University of Burgundy, GD 2368; ×8. C, *Heteraster delgadoi*, Comillas, Spain, Early Albian, MNHN R.63540; ×8. D, closed termination: *Epiaster henricii*, Aumale, Algeria, A. Devriès collection, University of Poitiers; ×9.

13. Axis of the petals: 0, straight; 1, anterior and/or posterior paired petals sinuous; 2, weakly curved near the apex.
14. Relative width of the paired petals: 0, narrow; 1, medium; 2, large.
15. Length of the frontal petal: 0, large, reaching the ambitus; 1, medium; 2, short.
16. Equipetality: 0, inequipetality (LI/LII < 0·55); 1, sub-equipetality (0·55 < LI/LII < 0·8); 2, equipetality (LI/LII > 0·8).

Ambulacral pores. In early spatangoids, four major types of pore pairs can be recognised. (1) Small isopores are oval diplopores showing a small interporal partition and a reduced neural canal. At the extreme these pores become punctiform and lose the neural canal (Text-figs 4B, 6B). Following Smith (1980*b*), small isopores could be associated with sensory tube feet. (2) Partitioned isopores are diplopores located within a trapezoidal to oval attachment area (Text-fig. 6A, C). These pores vary from rounded to triangular, with a large interporal protuberance and a well-defined neural canal. This type of pore is restricted to the frontal ambulacrum and is likely to be associated with tube feet used in burrowing or food transport. (3) Elongate diplopores are large transverse diplopores characterised by a flattened interporal partition, more or less asymmetrical pores and the absence of a neural canal (Text-fig. 6B–D). They occur in the petals and sometimes in the frontal ambulacrum. They are typical of respiratory tube feet. (4) Axially partitioned isopores have a large attachment area, a domed or bridged interporal partition, and a large
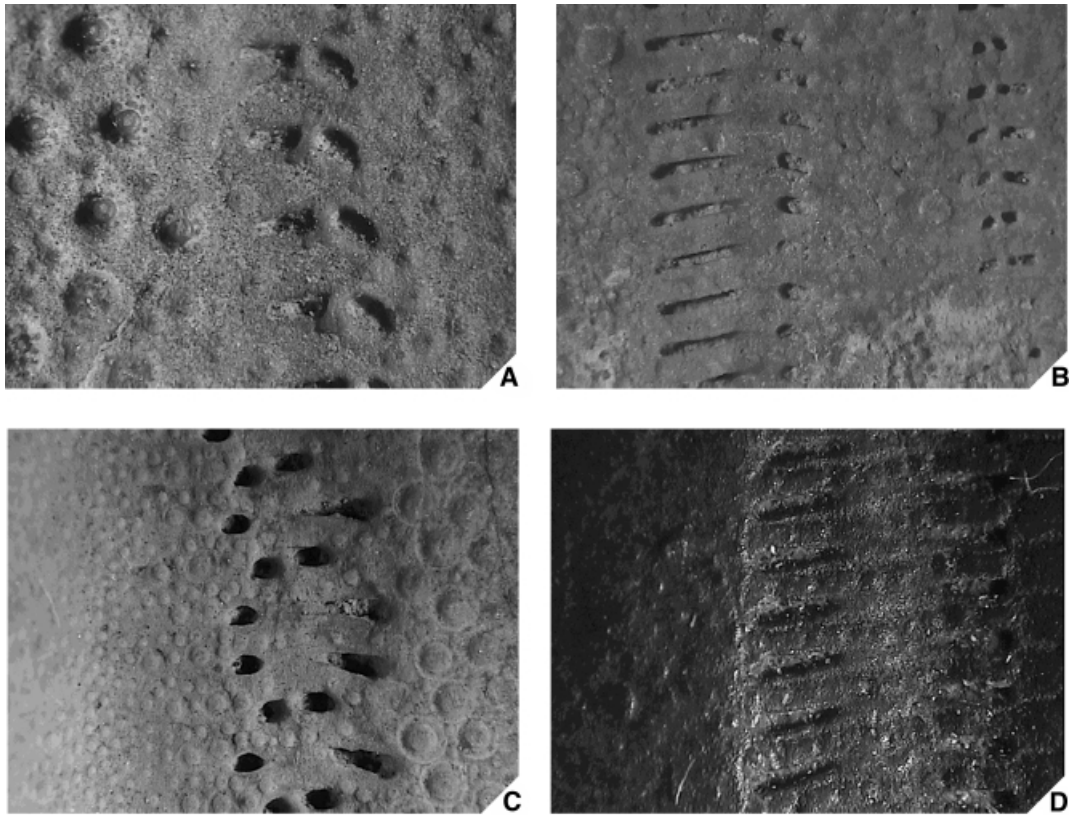
TEXT-FIG. 6. Diversity of pores in primitive spatangoids. A, partitioned isopores: *Toxaster ricordeaui*, Saint-Dizier, France, Barremian, University of Lyon, EM 10,000; ×17. B, association of small isopores with large elongate anisopores in the two branches of ambulacrum II of *Heteraster renngarteni*, Oglanlju, Turkmenistan, Barremian, S. Lobacheva collection, Museum of Historical Geology, University of St Petersburg; ×14. C, association of partitioned isopores with large elongate anisopores, involving alternation of the two kinds of pores, in the frontal ambulacrum of *Heteraster delgadoi*, Comillas, Spain, Early Albian, MNHN R.63540; ×14. D, elongate isopores with a wide interporal partition in *Epiaster maximus*, Guessa, Algeria, Cenomanian, A. Devriès collection, University of Poitiers; ×16.

neural canal (Text-fig. 8B–D). They are restricted to the phyllodes and correspond to sensory and food-gathering tube feet. The four types of pore are involved in two ontogenetic sequences: one for the oral part of the ambulacra, the other for the petals (Villier *et al.* 2001). The first sequence runs directly from small isopores to axially partitioned isopores through enlargement of the attachment area and strengthening of the interporal partition. The second sequence goes from small isopores to partitioned isopores, and then to elongate diplopores. This sequence implies a relative increase of pore length, an enlargement and then a reduction of the interporal partition and neural canal.

As shown above, the differentiation of ambulacra often induces variation in their pores: pores of the frontal petal frequently differ from those of the paired ones, and different pores can occur in each branch of the anterior petals but never in the posterior petals. Consequently, distinct characters have been retained for the frontal ambulacrum, anterior branch of the anterior paired petals, posterior branch of the same petals, and both branches of the posterior petals.

17. Type of pore pairs in the posterior branch of the anterior petals: 0, oval partitioned isopores; 1, asymmetrical elongate diplopores; 2, slit-like, symmetrical elongate diplopores.

18. Type of pore pairs in the anterior branch of the anterior petals: 0, oval partitioned isopores; 1, asymmetrical elongate diplopores; 2, slit-like, symmetrical elongate diplopores; 3, punctiform small isopores.
19. Type of pore pairs in ambulacrum III: 0, oval partitioned isopores; 1, asymmetrical elongate diplopores; 2, slit-like, symmetrical elongate diplopores.
20. Rectangular elongate diplopores in the frontal ambulacrum: 0, no; 1, yes.

The frontal ambulacrum of the genus *Heteraster* displays a highly characteristic heterogeneity of the pore pairs (Text-fig. 6c). In the simplest case, there is only variation in pore length without shape differentiation. More usual, however, is an alternation of two kinds of pore pairs (short, partitioned isopores and large, slit-like elongate diplopores). Heterogeneity can be increased by the occurrence of small triangular demi-plates bearing the short pairs.

21. Heterogeneity of pores in the frontal ambulacrum: 0, no; 1, yes.
22. Architectural heterogeneity of plates in the frontal ambulacrum: 0, no; 1, yes.

Apical disc. Recent Holasteroida show great variation in apical disc arrangement, especially in deep-sea taxa (Mooi and David 1996), but Cretaceous forms express a unique pattern. Paired ocular and genital plates are organised in two more or less symmetrical series joining medially according to Lovén's plan. Ocular plate III occupies a median position at the anterior edge of the apical system. Behind, meeting successively, are genital plates 2 and 3, ocular plates II and IV, genitals 1 and 4 and ocular plates I and V. This pattern is the so-called 'primitive elongated condition' for the two sister clades Spatangoida and Holasteroida (Fischer 1966). Much has been discussed about evolutionary trends leading from this primitive pattern to more derived ethmophract and ethmolytic patterns in the Spatangoida (Devriès 1963; Fischer 1966; Kier 1974; Smith 1984; Néraudeau 1994*a*). The general tendency is toward an antero-posterior compaction of the apical system and an increase in length of the madreporite, which fits in between other plates. Therefore, the madreporite separates successively the anterior ocular plates (ethmophract pattern), the posterior genital plates (semi-ethmolytic pattern), and the posterior ocular plates (ethmolytic pattern). The ethmolytic condition first occurred in the Late Cenomanian, but the two other patterns are represented in the species retained for the current analysis.

23. Apical disc: 0, ethmophract with ocular IV insert; 1, ethmophract; 2, semi-ethmolytic; 3, disjunct.

Interambulacrum 5 architecture. Architecture is very informative in phylogenetic analyses. For example, the number of ambulacral plates adjoining the labrum varies during ontogeny, but stays sufficiently constant in adults to provide phylogenetic information (Néraudeau 1990; Madon-Senez 1998; Moussa 1999). Unfortunately, only a few fossil sea urchins are sufficiently well preserved to reveal such characters. However, large plates, forming the plastron, pave the oral side of interambulacrum 5, which is easier to observe. Spatangoids are characterised by the possession of an amphisternous plastron in which the labrum (bordering the peristome) is followed by two more or less symmetrical and large sternal plates. Fischer (1966) recognised four plastronal patterns for the Spatangoida: protamphisternous, mesamphisternous, holamphisternous, and ultramphisternous. Early spatangoids express only the protamphisternous and mesamphisternous patterns, but it is possible to detail evolutionary steps for even the most primitive ones (Devriès 1963; Mintz 1968). From a protosternous ancestor, the plastronal architecture evolves mostly by an increase in size of the labrum and of the sternal plates and to a lesser extent by a differentiation of episternal plates. The labrum develops into a large triangular plate, or into an elongated rectangle. The sternal plates comprise the main part of the plastron. They tend to become more and more elongate and opposite each other. The two plates immediately behind the sternals are the episternals. Episternals differentiate relative to the ambital plates of interambulacrum 5 (i.e. pre-anals), growing larger and more symmetrical. The general trend towards a more and more symmetrical plastron holds for different lineages. This is particularly evident for lineages that became well established in the Late Cretaceous and Cenozoic (Kier 1974; McNamara 1987; Néraudeau 1990). On the other hand, the precise steps in the evolution of the plastron are not clearly and unambiguously set out for the radiating phase of the Early Cretaceous (Lovén 1874; Lambert 1892; Devriès 1960*a*, 1963). This weakness in our knowledge
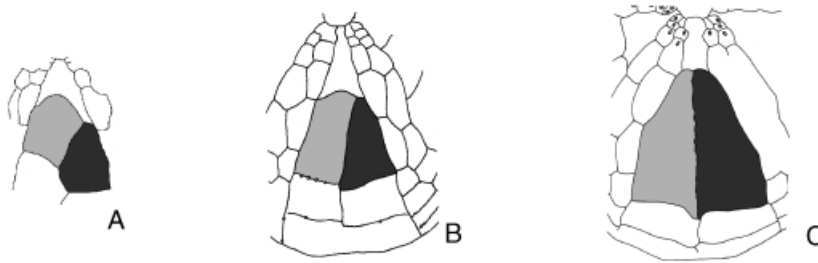
TEXT-FIG. 7. Architectural types of the plastron. A, protamphisternous with short sternals: *Toxaster rochi*, Algeria, Berriasian, A. Devriès collection, University of Poitiers. B, protamphisternous with elongate sternals: *Heteraster lepidus*, Ericeira, Portugal, Early Barremian, B. David collection, University of Burgundy, GD 1472. C, mesamphisternous symmetrical: *Heteraster texanus*, Clifton, Texas, Comanche Peak Formation, MNHN R.11897.

of such an important feature is due to the lack of precise phylogenetic hypotheses for this phase of spatangoid evolution. Indeed, some parallelism can be suspected between the main clades, and it is not clear when this may have first occurred.

To take into account the changes in plastronal plate pattern in early spatangoids, we have attempted to code one character (Text-fig. 7). The first state is characterised by short, quadrangular sternal plates, both joining the labrum. The right sternal plate (5.b.2) is larger and develops a convexity that indents the labrum. The second state shows an asymmetrical plastron with plastronal plates that are distinctly elongate. Plate 5.b.2 is trapezoidal and always more developed than plate 5.a.2, which is triangular. Their anterior junction is displaced toward the left side of the sea urchin, either against the labrum or against the adjacent ambulacral row (V.b). The third state corresponds to more symmetrical sternal plates, becoming triangular in shape and joining the labrum on the axis of symmetry.

24. Plastron: 0, protamphisternous with short sternals; 1, protamphisternous with elongate sternals; 2, mesamphisternous symmetrical.

The number of plates between the peristome and the periproct (i.e. labrum, sternal, episternal, pre-anal, and first anal plates) was counted in column 5.a. This count records the number of plates produced before the removal of the anus from the apical disc during early ontogeny.

25. Number of plates between anus and sternal plates: 0, 8 plates; 1, 7 plates; 2, 6 plates; 3, 5 plates.

Peristome. The position of the peristome is generally retained in species diagnoses even if it is a highly allometric feature (Devriès 1960*b*; David 1980). The peristome shifts progressively from a central position in early ontogenetic stages to a more anterior one in adults. Variations still occur in adult forms. Measurements of the relative position of the peristome with reference to the posterior end of the test show intraspecific variations, which are of the same order of magnitude as the interspecific ones. Therefore, this parameter has not been taken into account. In the most derived taxa, the shape of the peristome also undergoes important ontogenetic changes (Gordon 1926; Néraudeau 1990). In juveniles, the peristome is flush with the test and pentagonal in shape. With growth, the peristome becomes depressed, the labrum gets wider, and the plastron forms a keel on the oral side of the test. In mature forms, the labrum develops over the peristomial edge, and the peristome becomes reniform. The shape of the peristome is quite stable within a given species, at the mature stage. Among primitive spatangoids, it displays important variations that mimic the ontogenetic stages (Text-fig. 8).

Three characters referring to the orientation, the outline, and the development of the labrum describe the shape of the peristome.

26. Peristome orientation: 0, flat; 1, oblique; 2, strongly oblique and curved.
27. Shape of the peristome: 0, rounded to pentagonal; 1, transverse pentagon; 2, reniform.
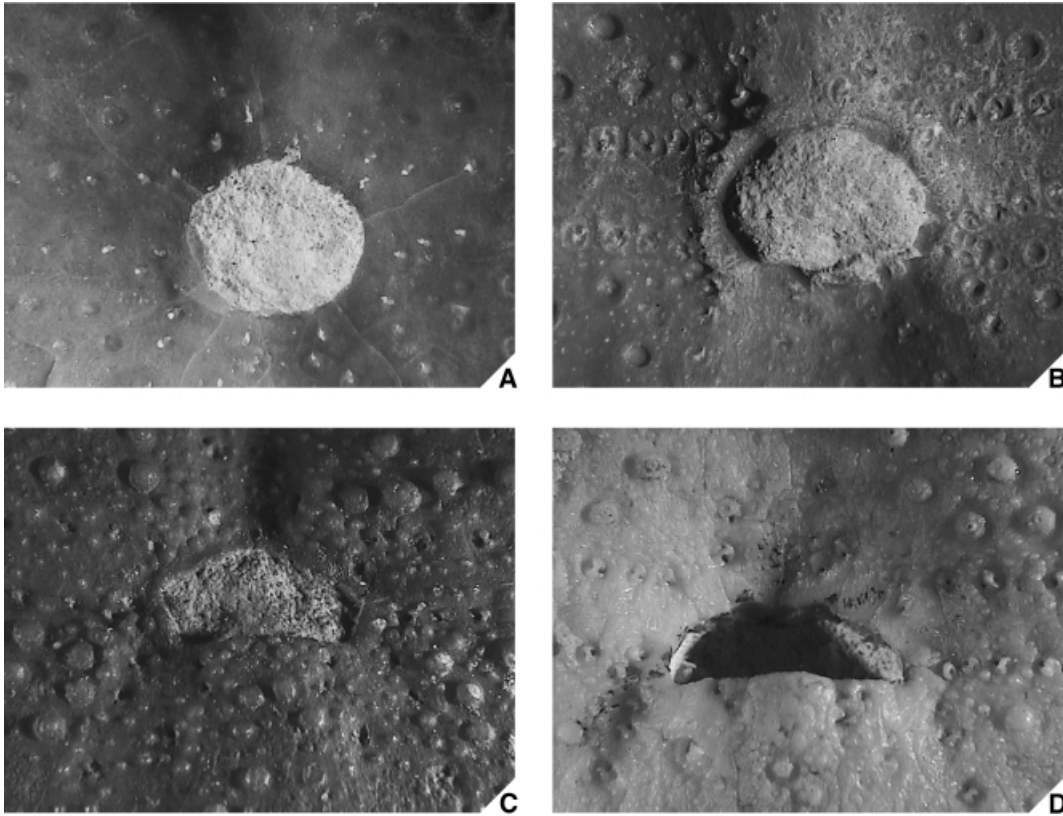
TEXT-FIG. 8. Shape of the peristome. A, round, flattened peristome of *Heteraster texanus*, Clifton, Texas, Comanche Peak Formation, Albian, MNHN R.11897; ×9. B, rounded, oblique peristome surrounded by a depressed fringe in *Epiaster heberti*, Djebel Chegorig, Algeria, A. Devriès collection, University of Poitiers; ×7. C, wide pentagonal peristome with a straight and wide peristomial edge to the labrum in *Epiaster henricii*, Aumale, Algeria, Cenomanian, A. Devriès collection, University of Poitiers; ×6. D, reniform, concave peristome with an overhanging labrum in *Micraster decipiens*, origin unknown, Turonian, B. David collection, University of Burgundy, GD 2370; ×6.

28. Labrum: 0, peristomial edge as large as in other interambulacra; 1, peristomial edge straight and wide; 2, overhanging the peristome.

Test shape. Fischer (1966) considered that an important trend in spatangoid evolution was the deepening of the ambulacra. When species adopted an infaunal mode of life, deepening of the petals improved the protection of respiratory tube feet and deepening of the frontal ambulacrum into a groove provided a channel for water flow and food gathering (de Ridder and Lawrence 1982). The efficiency of the anterior groove is improved when it continues down to the mouth. In this case a frontal notch indents the ambital outline. All these features are clearly expressed in many derived spatangoids (Mortensen 1951), but they are generally weak in early spatangoids and therefore especially hard to estimate.

We have retained four characters. Paired petals can be slightly or deeply depressed on the surface of the test. At their distal extremity, the depression can end progressively or in a steep slope. The principle of coding for the anterior groove and for the frontal notch is quite simple (depth of the concavity), but it is hard to assess and corresponds to small differences between species. Such characters must *a priori* be considered with caution.
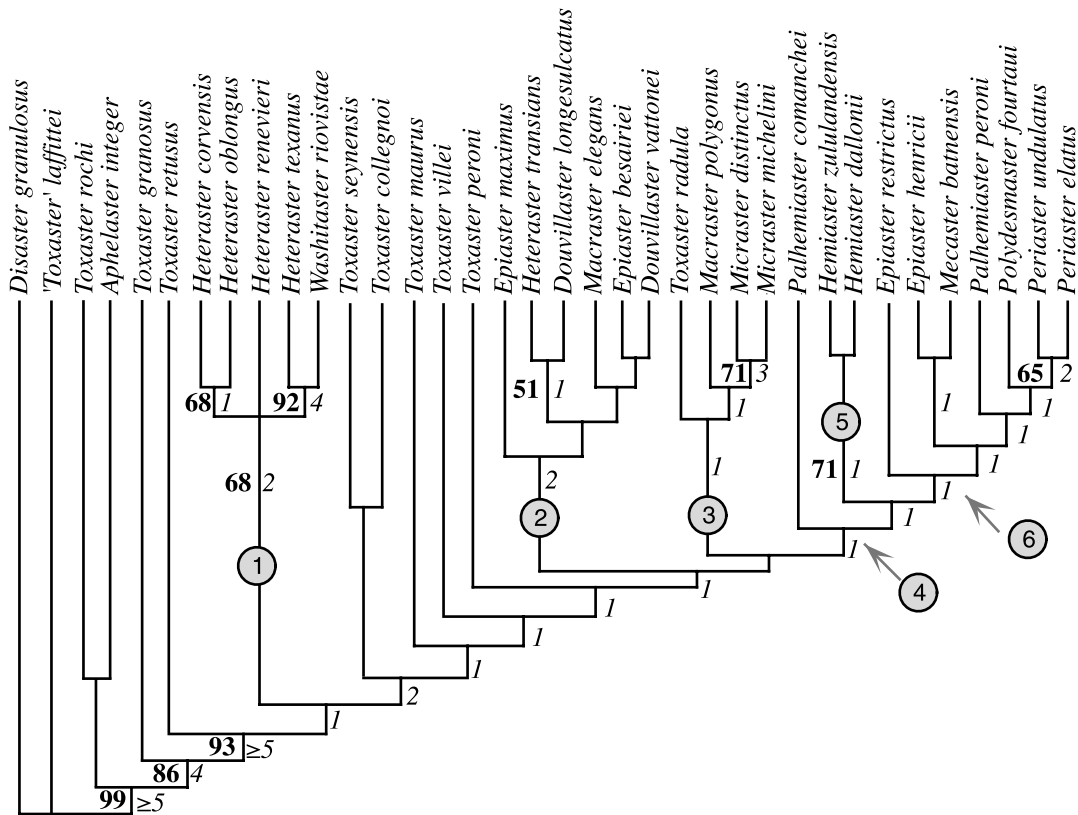
TEXT-FIG. 9. Fifty per cent Majority Rule consensus tree for 128 equally parsimonious trees of 145 steps. *Disaster elongatus* and '*Toxaster*' *laffittei* are outgroups. Encircled numbers designate clades to facilitate description of the tree. Numbers in bold indicate bootstrap values and numbers in italic font correspond to Bremer support (decay index) on nodes.

29. Depression of the paired petals: 0, null; 1, slightly concave; 2, deep.
30. Termination of the petals: 0, progressive decrease of depth; 1, steep slope.
31. Frontal groove: 0, null; 1, slightly concave; 2, large and deep.
32. Anterior notch: 0, rounded; 1, weak indentation; 2, strong indentation.

Other test characteristics are frequently used in taxonomy, and were included here (Devriès 1955, 1963; Smith 1984; Néraudeau 1994*b*; Jeffery 1999).

33. Posterior end of the test: 0, rounded; 1, truncated; 2, prominent rostrum.
34. Position of the apical disc: 0, central or anterior; 1, posterior.
35. Shape of the periproct: 0, rounded or wider than high; 1, high with pointed radial tips.

RESULTS

Resulting trees

Matrix optimisation found 128 most parsimonious trees with a length of 145 steps. Description and analysis of the phylogeny are based on the Majority Rule tree on which almost all the nodes are fully supported (Text-fig. 9). Uncertainties in tree topology concern: (1) the relative position of *Aphelaster*

integer and *Toxaster rochi*; (2) the branching of *Heteraster* species (clade 1 on Text-fig. 9); (3) the relative position of *Toxaster collegnoi* and *Toxaster seynensis*; (4) the branching between clades 2, 3 and 4; (5) the relationships between the six species of clade 2. Despite a large proportion of fully supported nodes (22 out of 29), computed indexes show quite low values: CI = 0·43, HI = 0·57, RI = 0·76, and RC = 0·33. Such low values are explained by a large number of characters expressing homoplastic changes (27 out of 35).

Congruence with stratigraphical data

Calculated indexes (SCI = 0·65, RCI = 43 and GER = 0·85) indicate a relatively high average congruence between the majority rule tree topology and the stratigraphical record. The test of permutation, as provided by the GHOSTS software (Wills 1999*b*), confirms a significant deviation from random attribution of stratigraphical data (with 0·2% uncertainty). Moreover, the values obtained fall within the ranges given by Benton *et al.* (1999) for main fossil groups. The inconsistency comes mostly from the internal nodes of clade 4, which associates species known from the Aptian to the Cenomanian. This situation can come from the tree itself, from the incompleteness of the fossil record, or as an artefact of species sampling.

Basal apomorphies

Since its first definition, the order Spatangoida has been classically based on three apomorphies: protamphisternous to amphisternous plastron, ethmophract to ethmolytic apical system, and petals. The dataset analysed herein provides seven apomorphies at the base of the Spatangoida, even if all the implied characters change homoplastically in more derived taxa (Text-fig. 10). These apomorphies encompass characteristics of the ambulacra (differentiation of the petals, change of the apical system, and especially in the pores which become larger, and rectangular in the petals), but do not concern the plastron. Therefore, this result departs slightly from the classical definition of the order. This is not surprising if we consider the variability of the architecture of the plastronal area in primitive spatangoid-like echinoids from the Late Jurassic and Early Cretaceous. The set of apomorphies obtained clearly prevents placement of '*Toxaster*' *laffittei* among the Spatangoida, confirming the hypothesis originally proposed by Solovjev (1989).

Status of clades and taxa

Genus Toxaster. Lower branches of the tree and branches between clades 1 and 2 show a pectinate distribution of *Toxaster* and *Aphelaster* species. The genus *Toxaster* appears as a paraphyletic grouping distributed in three subsets. Such a pattern for *Toxaster* reflects the weak definition of the genus, mostly based on plesiomorphic characters (e.g. semi-petaloid paired ambulacra, ethmophract apical system), including the absence of characteristics (no fascioles).

Former authors have identified *Toxaster* lineages on stratigraphic and phenetic grounds (Lambert 1931; Devriès 1960*a*; Rey 1972; Masrour 1987): (1) *T. granosus – T. granosus kiliani – T. lorioli*; (2) *T. seynensis – T. collegnoi – T. radula*; and (3) *T. maurus – T. villei – T. peroni* (the so-called 'cavipetal' group of Lambert). The trends recorded within these lineages mostly involve changes in general shape and ambulacra. Devriès (1963) noticed that such evolutionary trends are common in many spatangoid groups, and that they correspond to functional adaptations to burrowing. The topology of the cladogram allows only partial recognition of the previously identified trends. *T. seynensis* and *T. collegnoi* are grouped in a polytomy, which does not contradict the suggested lineage. On the other hand, *T. radula* is placed far up in the cladogram. A reappraisal of the position of *T. radula* to fit the requirements of the lineage would cost at least two steps. Such an amount of homoplasy should be a reasonable compromise, but we prefer to accept the original topology. On the cladogram, the cavipetal group *T. maurus*, *T. villei* and *T. peroni* appears as a paraphyletic subset consistent with a hypothesis of lineage continuity. Moreover, the characters supporting the nodes (shape of the petals) are among those used by Lambert (1931) and Devriès (1960*a*). The evolutionary trend underlying this lineage seems to be peramorphic.

Position of Aphelaster. The genus *Aphelaster* was erected by Lambert (1920*a*) for conical toxasterids with a rounded outline and long and identical paired petals. In this analysis, if characteristics of the general
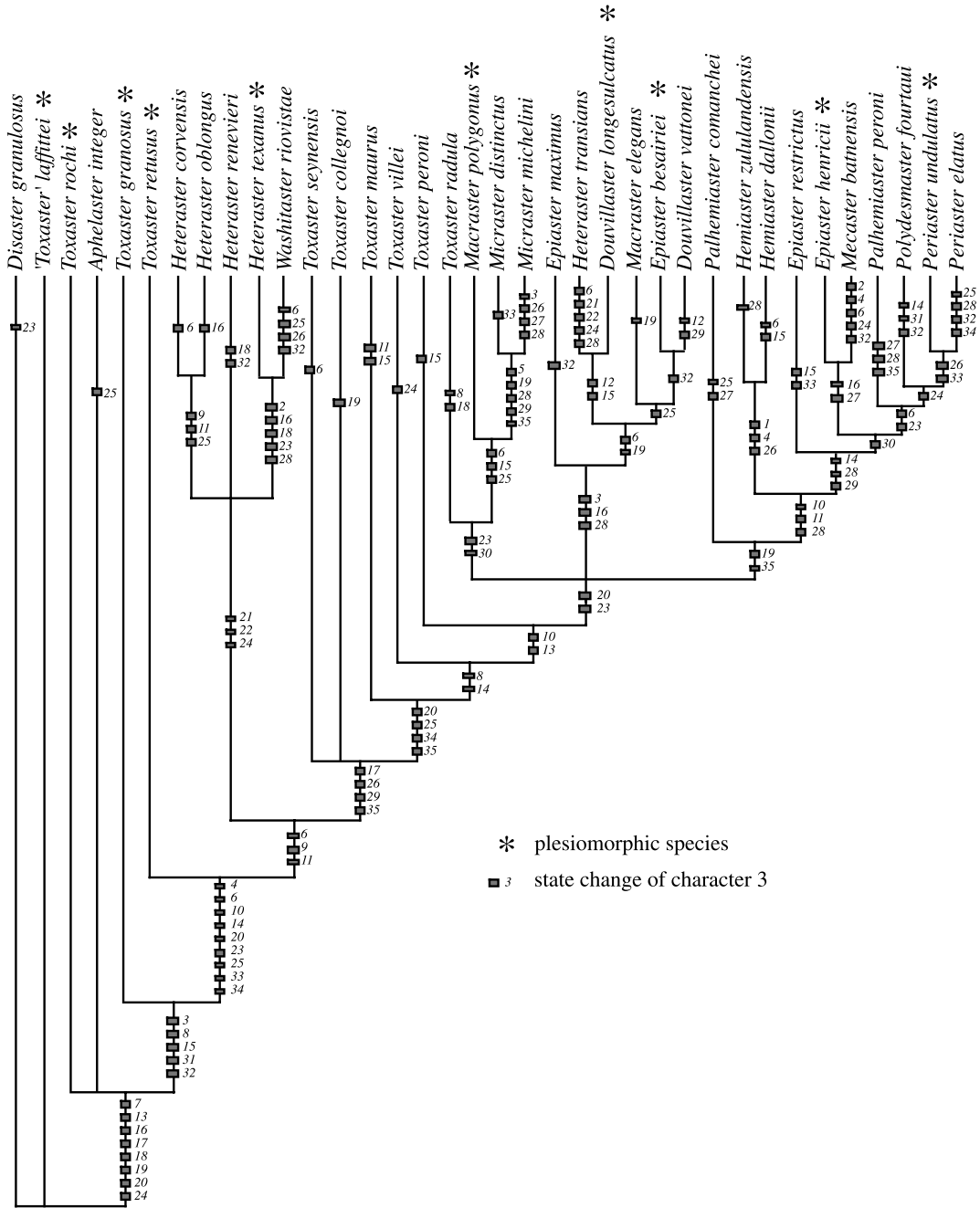
TEXT-FIG. 10. List of character-state changes at the nodes of the majority rule consensus tree. Two badly supported nodes of the 50 per cent majority rule consensus are treated as polytomy.

shape are excluded, the phylogenetic position of *A. integer* (from the Valanginian of the peri-Mediterranean region) cannot be unambiguously determined. The species appears to be closely related to *Toxaster rochi*, differing only by the number of plates between the sternal plates and the periproct. The

other species assigned to this genus (*A. serotonus* from the Barremian of Japan) is so poorly known that it is impossible to tell if it actually belongs to the genus. Lambert (1931) proposed a phylogenetic link between *T. rochi* and *A. integer*. Later, Devriès (1960*a*) retained this link and synonymised *Aphelaster* with *Toxaster*. Our phylogeny does not contradict this proposition, and we follow Devriès' advice to place *A. integer* within *Toxaster*.

Heteraster clade. Clade 1 fits in with the genera *Heteraster* and *Washitaster*, with the exception of the species *H. transians*. This topology corroborates the synonymy between *Washitaster* and *Heteraster* proposed by Cooke (1955) and Devriès (1960*a*). *H. transians* branches into the clade *Douvillaster–Macraster*. The generic attribution of this species must thus be reconsidered. Once *Macraster*? *transians* has been discarded, the genus *Heteraster* appears as a well-defined monophyletic group based on a flattened shape, a rectangular outline and, most importantly, on alternating short and elongate pores in the frontal ambulacrum. The isolated position of *M.*? *transians* means that the diagnostic character of pore heterogeneity in the frontal ambulacrum appeared independently and by convergence in the genus *Heteraster* and in the *Douvillaster–Macraster* group. However, pore morphology differs conspicuously between *M.*? *transians* and *Heteraster* species. The elongate diplopores are asymmetrical in the latter, while they are slit-like and nearly symmetrical in *M.*? *transians*. It is interesting to note that differences in length of the external pores in the anterior ambulacrum appear earlier as an occasional intraspecific variation in at least two primitive *Toxaster* species (*T. villei*, *T. rochi*). However, such variations are never associated with morphological differentiation of the pores, and the genus *Heteraster* can be considered as the first clade that fixes and develops the character.

Heterogeneity between successive pores can also affect the paired petals. Devriès (1955, 1960*a*) and Rey (1972) accurately described heterogeneity in the paired petals as intraspecific variations in some Lower Cretaceous species: *Heteraster oblongus*, *H. pomeli*, *H. peroni*, *H. tissoti*, *M.*? *transians*, *Toxaster villei*, *T. peroni*, *T. collegnoi* and *Mecaster brahim*.

Douvillaster–Macraster clade. Clade 2 groups species from the genera *Douvillaster*, *Macraster*, *Epiaster* and *Heteraster*. As a whole, this clade is well supported by the analysis, despite the fact that its ingroup topology remains equivocal. It confirms the *Douvillaster-Macraster* relationship formerly suggested by Neumann (1999), although their relationship is not exclusive. The clade unites spatangoids of medium to large size with an inflated test bearing large and wide petals. The anterior petals are about the same size as the posterior ones. The tuberculation is homogeneous, and made up of loose, small tubercles. These morphological features easily distinguish members of the clade from other primitive spatangoids.

Originally erected for North American toxasterids (Roemer 1888), the genus *Macraster* was later extended to European and North African species (Lambert and Thiéry 1924, 1925; Lambert 1931). The American species are quite similar in aspect: large size, flattened oral side, rounded to heart-shaped ambitus, and long, slender petals. Other species assigned to *Macraster* share only some of these characters. Their taxonomic position is uncertain, and needs to be reappraised. For example, Lambert and Thiéry (1924) attributed the species *polygonus* to the genus *Macraster* only on the basis of its flattened shape and its large size. Subsequent authors never challenged this attribution (Villalba-Curras 1993; Néraudeau and Breton 1993). However, in our tree *Macraster polygonus* does not fall inside the *Douvillaster–Macraster* clade.

Additional confusion exists between *Macraster* and *Douvillaster*, as suspected by Kier (1984). In the classifications of Lambert (1920*b*) and Fischer (1966), the two genera are differentiated only by the depth of the petals and the morphology of pores in the frontal ambulacrum (pore pairs are arranged in chevrons in *Macraster*, while they are transversely elongated in *Douvillaster*). In fact, the ontogenetic sequence of the pores of the frontal ambulacrum of *Douvillaster* shows a transition from a *Macraster*-like to a *Douvillaster*-like pattern, and some large specimens of the American *Macraster* bear *Douvillaster*-like pores. Moreover, shape differences between the American and the African species of *Macraster* (such as *M. besairiei*) and some species of *Douvillaster* are very tenuous (even for some doubtful '*Epiaster*' species such as '*E.*' *maximus*). Therefore, the petaloid ambulacrum III could constitute the only remaining diagnostic character for the genus *Douvillaster*.

These comments highlight the confusing taxonomic situation that currently exists between *Douvillaster* and *Macraster*. The hypothesis supported by the cladogram (Text-fig. 9) does not fully solve the question since species of *Douvillaster* and *Macraster*, as well as large *Epiaster* species, are inter-mixed in clade 2.

Micrasterina clade. Clade 3 contains *Toxaster radula*, *Macraster polygonus*, *Micraster michelini*, and *M. distinctus*. As defined by the topology of the tree, this clade groups one toxasterid, two typical micrasterids, and *Macraster polygonus*, which has been successively attributed to micrasterids (d'Orbigny 1853; Savin 1903) and toxasterids (Lambert and Thiéry 1924). It seems to foreshadow the suborder Micrasterina, albeit modified by the association of former toxasterids. Traditionally Micrasterina has been rooted as the sister clade of *Toxaster radula*. *T. radula* bears a well-developed and nearly complete parafasciolar ring around the test (Néraudeau *et al.* 1998). In contrast, only short, thin rows of aggregated miliaries on the sides of the test remain in primitive Micrasterina. These probably evolved from a *Toxaster*-like species by reduction of the peripetalous fascioles, enlargement of the test, and by a straightening and increase in symmetry of the petals. Primitive Micrasterina lack the defining characters of more recent members of the group, such as ring-shaped sub-anal fasciole, prominent reniform labrum, and the typical heart-shaped outline of the *Micraster* species of the Chalk. To include its oldest members, the suborder Micrasterina must be redefined according to the present phylogenetic scheme. We propose herein to extend the clade Micrasterina so as to include all taxa comprising clade 3 of the tree.

Our phylogenetic hypothesis does not support the grade genus *Epiaster*, which is spread across clades 2 and 4. D'Orbigny (1855) established *Epiaster* in 'livraison 12' of the Paléontologie Française (pp. 177–192). He recognised eight nominal species but described only four (*E. polygonus*, *E. trigonalis*, *E. koechlinanus*, and *E. distinctus*), the four remaining being published later in the same year, in 'livraison 13' (*E. aquitanicus*, *E. crassissimus*, *E. tumidus*, and *E. varusensis*). In his original description, d'Orbigny did not designate a type species, and this lack has dramatic consequences for the use of the genus. Lambert (1895) proposed *E. crassissimus* as the type species of *Epiaster*. However, Lambert and Thiéry (1924) suggested *E. trigonalis*, arguing that *E. crassissimus* was not part of the species originally listed in d'Orbigny (1855). Since then, *E. trigonalis* was considered as the type species until Stokes (1977) re-established *E. crassissimus* as the supposedly correct type species. Later, Smith (1988) criticised Stoke's position. We state here the type species of *Epiaster* d'Orbigny 1855 is *Micraster trigonalis* Desor, *in* Agassiz and Desor 1847, by subsequent designation of Lambert and Thiéry (1924, p. 477).

In fact, different usages of the genus have been proposed. (1) To consider the genus *Epiaster* valid, eventually redefined on other features (Pomel 1883; Lobacheva 1968; Stokes 1977; Villalba-Curras 1993): this conservative position purports to consider *Epiaster* as a polyphyletic evolutionary grade of cordiform toxasterids with rather symmetrical and flush petals. (2) To synonymise *Epiaster* species as a whole with *Heteraster* (Fischer 1966) or the non-*Micraster*-like species only (Smith 1988): this position is related to the confusion over the type species. Fischer (1966) noted that *E. trigonalis* (which he considered as the type species of the genus) shows an alternation of short and slender pores in the frontal ambulacrum, and placed this species within *Heteraster*, thus synonymising the two genera. Some more recent papers have followed this proposition (Brito and Ramirez 1974; Smith 1988). We observed several specimens of *Epiaster trigonalis* from the type locality (d'Orbigny and Lambert collections in the Muséum National d'Histoire Naturelle). This material shows a frontal ambulacrum with single row of circumflex-like pores and does not display any alternating pattern. Consequently, '*Epiaster*' species as a whole cannot be considered as *Heteraster* species. (3) To put *Micraster*-like '*Epiaster*' species without a subanal fasciole in the genus *Micraster* (Coquand 1880; Smith 1988; Néraudeau and Moreau 1989; Néraudeau and Mathey 2000) and other species in the genera *Douvillaster*, *Hemiaster* or *Macraster* according to the species: this solution appears to be the most consistent with the phylogenetic results, but cannot be adopted without an ambitious revision dealing with all of the species formerly attributed to *Epiaster* and encompassing at least primitive *Micraster*, some Hemiasterina, as well as *Douvillaster* and *Macraster*. However, a part of the work has been done in some papers. Following its micrasteriform test and petal shape, Smith (1988) attributed the species *distinctus* to the genus *Micraster*, considering that the lack of subanal fasciole was not an obstacle to this option. This opinion was confirmed by Néraudeau and Moreau (1989), who considered the genus *Epiaster* as a subgenus of *Micraster* for the Cenomanian *Micraster*-like species

M. (*E.*) *distinctus* and *M.* (*E.*) *crassissimus*, without a conspicuous subanal fasciole. This option follows the more or less clear point of view of d'Orbigny (1855), Lambert and Thiéry (1924), Stokes (1977) and Smith (1984). Then, Néraudeau *et al.* (1998) noted that the subanal fasciole of younger species of *Micraster*, such as the Coniacian *M. decipiens*, is sometimes inconspicuous (morphotype *renati* of *M. decipiens*). Finally, Néraudeau and Mathey (2000) reconsidered the generic status of several species previously placed in '*Epiaster*' with, on the one hand, *Micraster* (*E.*) *dartoni*, *M.* (*E.*) *distinctus* and *M.* (*E.*) *renfroae* placed in the genus *Micraster* and, on the other hand, *Macraster angolensis*, *M. besairiei*, *M. boipebensis* and *M. catumbellensis* in the genus *Macraster*.

Hemiasterina clade. The large clade 4 includes species of the genera *Palhemiaster*, *Hemiaster*, *Mecaster*, *Periaster* and two species previously referred to *Epiaster* that must be attributed to another genus. Except for '*Epiaster*', all of these genera were classically included within the suborder Hemiasterina. Ingroup clades 5 and 6 correspond to traditionally recognised genera (respectively *Hemiaster*, *Mecaster* and *Periaster*) with *Palhemiaster*, *Polydesmaster*, or '*Epiaster*' species at their base.

Hemiaster clade. The phylogenetic analysis clearly separates the genus *Hemiaster* (clade 5) from other members of clade 4. It confirms the diphyletic pattern recognised by Néraudeau (1990) who distinguished the lineage of *Hemiaster s.s.* (e.g. *H. minimus* and *H. bufo*) from the lineage of *Mecaster* (e.g. *M. latigrunda* and *M. fourneli*). As the family Hemiasteridae then becomes, at best, paraphyletic, Néraudeau (1994*b*) kept only the first lineage in the Hemiasteridae and put *Mecaster* and *Palhemiaster peroni* in an *incertae sedis* family. In the present analysis, the meaning of the family Hemiasteridae is restricted to the *Hemiaster* clade of the tree. The primitive species of *Hemiaster s.s.* differ from other early spatangoids, including the expected ancestor *H. peroni* (Devriès, 1960*a*; Néraudeau 1990) in several characters: the development of a peripetalous orthofasciole (corresponding to a parafasciolar ring in the most primitive forms such as *H. zululandensis*); the loss of the protofasciolar batch at the end of the frontal ambulacrum; a reniform peristome; and a high density of tubercles all over the test. Moreover, members of the *Hemiaster* clade are generally recognised (Néraudeau 1994*a, b*) by their globular shape with a high test and a faint or absent anterior notch and anterior and posterior petals conspicuously unequal with always short posterior ones.

Mecaster-Periaster clade. Clade 6 comprises various forms previously classified in the families Toxasteridae, Hemiasteridae, and Schizasteridae. This clade appears to be organised in several sub-units, which are supported by few apomorphies.

Mecaster batnensis and *Epiaster henricii* constitute a small clade, which is defined by the association of the paired ambulacra of similar length with an enlarged pentagonal peristome. They also share an angular ambital outline with two conspicuous angles at the posterior end of the ambitus and a deep anterior notch. We suggest that this clade corresponds to the genus *Mecaster* and, consequently, that *Epiaster henricii* is a *Mecaster*. From the Cenomanian, the genus *Mecaster* gave rise to an important radiation, mostly along the Tethyan margins (Zaghbib-Turki 1989; Néraudeau, 1990, 1994*a*; Smith *et al.* 1990; Néraudeau and Floquet 1991; Néraudeau *et al.* 1995; Néraudeau and Mathey, 2000).

Our phylogenetic analysis identifies a clade that groups *Polydesmaster fourtaui* and *Palhemiaster peroni* with the *Periaster* species. *Palhemiaster peroni* is separated from *Mecaster* by a single, highly homoplastic character (reversal of architecture of the apical system to an ethmophract pattern). The topology of the tree is, thus, not drastically different from the previously suggested position of *P. peroni* as an ancestor of *Mecaster* (Néraudeau 1990, 1994*b*). *Polydesmaster fourtaui* has always been considered a toxasterid (Lambert 1920*a*, Fischer 1966), but its attribution to toxasterids was mostly based on the lack of a continuous peripetalous orthofasciole. On the other hand, its position at the top of the tree is supported by many characters, which are not contradicted by autapomorphic reversals. This strongly suggests close relationships with *Periaster*.

Despite being morphologically quite different in shape, the two species of *Periaster* appear as sister taxa. *Periaster* is classically considered as the oldest member of the family Schizasteridae (Mortensen 1950; Fischer 1966; Néraudeau 1990). However, Néraudeau (1994*a*) and Moussa (2001) have pointed out some inconsistency in the use of the name *Periaster* by several authors (Devriès 1973; Zaghbib-Turki

1987). This name has been used either for true *Periaster* species (close to the type species *P. elatus*), or to designate *Mecaster* specimens with a supplementary latero-anal fasciole in fine-grained sediments. Lambert (1931) proposed to maintain *Mecaster* specimens with two fascioles in this genus (and not in *Periaster* or *Linthia*), only distinguishing the specimens with two fascioles as a '*bifasciata* stage' or a *bifasciata* variety. Finally, Néraudeau (1994*a*) concluded that *Mecaster* at the '*bifasciata*' stage are typical African species while true *Periaster* are restricted to south-west Europe, and that the two morphological groups are convergent and not directly related.

TAXONOMIC CONCLUSIONS

Results from our phylogenetic analysis support some long-standing taxonomic groupings, but also present important new evidence from which the history and taxonomy of families and genera can be revised. In reference to previous classifications, the tree confirms the validity of the suborders Micrasterina and Hemiasterina erected by Fischer (1966), the paraphyletism of the Toxasterina and Toxasteridae suggested by Smith (1984), the diphyletism of the family Hemiasteridae (Néraudeau 1990, 1994*b*), and the clade *Macraster* plus *Douvillaster* (Neumann 1999). On the other hand, the tree suggests that the genus *Heteraster* is monophyletic rather than polyphyletic, as implied by the evolutionary scenarios of Devriès (1960*a*) and Rey (1972). Our phylogenetic hypothesis leads us to reconsideration of the composition of several groupings at the generic or family levels (Text-fig. 11), which is necessary before a complete systematic revision of several terminal clades can be undertaken.

Toxasteridae. The family Toxasteridae, and most of the genera it includes, are mainly defined on plesiomorphies that *de facto* cause the paraphyly of these taxa. In the basal groups of the Spatangoida, the only well-defined taxa are those with a distinctive, derived shape like *Aphelaster* or obvious anatomical features like *Heteraster*. Fischer (1966, p. U651) noticed that 'the genus *Toxaster* is diverse and requires subdivision'. Its paraphyletic status is not in doubt, but cannot be resolved without a complete revision of all its species. As a whole, the family Toxasteridae has to be considered as the stem group for all the more derived Spatangoida but cannot be viewed as a 'natural phyletic group', as inferred by Fischer (1966).

Douvillaster-Macraster clade. The group *Douvillaster-Macraster* has only very recently been identified (Neumann 1999). Our topology supports this group with a level of confidence similar to groupings such as the Micrasterina, Hemiasterina or Hemiasteridae. We provisionally propose uniting *Epiaster maximus*, *Heteraster transians*, all species referred to *Douvillaster* and all species referred to *Macraster* in a single genus, *Macraster* Roemer, 1888. This position is also supported by the similar stratigraphic range of the former genera *Macraster* and *Douvillaster*, by the instability of the specific attributions between those two genera, as well as by the weakness of their distinctive features (see above).

Micrasterina. We consider all taxa contained in clade 3, or subsequently derived forms, as members of the Micrasterina. The primitive member of the suborder probably looked like *Toxaster radula*, even if this species is more recent (Albian) than the earliest recorded *Micraster polygonus* (mid Aptian). All the Micrasterina retained by the present analysis correspond to early members of the order, and do not belong to families subsequently derived from Micrasteridae. All other families of Micrasterina appeared later (Fischer 1966; Smith 1984). Consequently, the family Micrasteridae becomes *de facto* paraphyletic and is basal to all of the suborder Micrasterina.

Hemiasterina. According to the topology of the cladogram (Text-fig. 9), all taxa in clade 4 are considered to be members of the Hemiasterina. This clade encompasses ordinary hemiasterids and schizasterids along with some species formerly referred to as toxasterids (*Epiaster restrictus* and *E. henricii*). This undermines the reliability of fascioles as features for the definition of genera or families.

The classical distinction between Hemiasteridae and Schizasteridae relies principally upon the fascioles. The Hemiasteridae is characterised by a unique peripetalous fasciole, while the Schizasteridae bears two fascioles, a peripetalous and a latero-anal. However, the peripetalous fascioles of hemiasterids
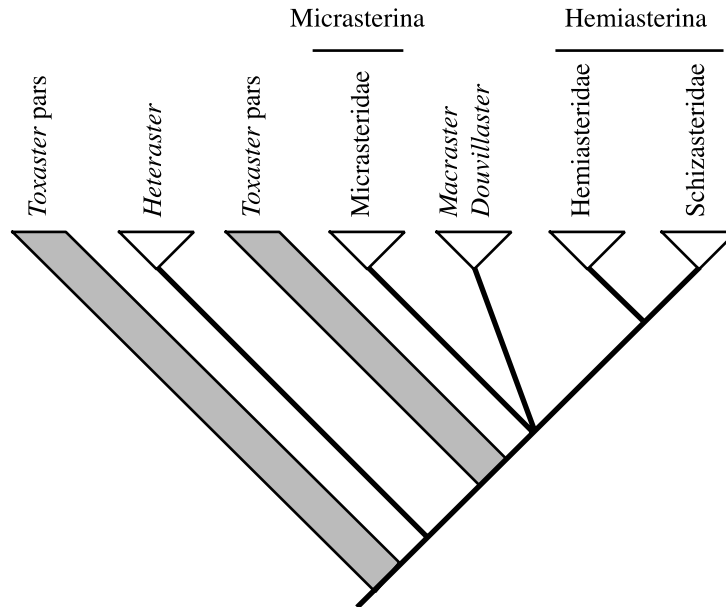
TEXT-FIG. 11. Branching patterns of clades and taxa retained after revision. Grey trapeziums indicate paraphyletic taxa, and white triangles indicate monophyletic taxa.

and schizasterids cannot be considered homologous. The fasciole of hemiasterids is made of a single ring encircling the petals. In schizasterids, the fasciole is composed of two branches that fuse together in early ontogeny, thereby constituting an apparently continuous peripetalous fasciole (Mortensen 1907; Mespoulhé 1992).

Néraudeau (1994b) redefined Hemiasteridae, restricting the family to taxa with short posterior petals, and excluding *Mecaster*. This is congruent with the presence of a true peripetalous fasciole, and is supported by the present topology (see above).

The situation is more confusing for the other Hemiasterina as fascioles can no longer be considered reliable as indicators of taxonomic relationships, although they have previously played a large role in supporting certain taxa (Lambert and Thiéry 1924; Mortensen 1950; Fischer 1966 *inter alia*). The peripetalous orthofascioles expressed in the genera *Mecaster* and *Periaster* seem similar, but they are, in fact, homoplastic because the two genera originate from two different ancestors (*Epiaster* or a *Palhemiaster*-like species) with large parafasciolar bands. The genus *Periaster* is considered the oldest member of the family Schizasteridae in its traditional sense. The earliest species of the genus, *Periaster undulatus* and *P. elatus*, show diverse fasciolar patterns, from simple or multiple parafasciolar textures to conspicuous and continuous orthofascioles. At the base of the *Periaster* clade, *Palhemiaster peroni* and *Polydesmaster fourtaui* display similar parafasciolar strips associated with discontinuous orthofasciolar bands.

Therefore, the capability of constructing two orthofascioles (peripetalous and latero-anal) seems to be an apomorphy for the entire clade 6, even if this capacity is not fully expressed in some primitive members. Accordingly, the simplest solution is to redefine the Schizasteridae as clade 6. In such a hypothesis, Schizasteridae constitutes a monophyletic group containing all the derived forms with clear latero-anal and peripetalous orthofascioles, as well as primitive forms with a facultative latero-anal fasciole (e.g. *Mecaster*) or with predominant parafasciolar textures (e.g. *Palhemiaster*). Within this family, we maintain *Palhemiaster* as a paraphyletic grouping until a more complete revision is undertaken.

The taxonomic conclusions proposed herein represent a compromise between two main goals: to emphasise monophyletic taxa, and to maintain continuity with traditional terms and usage rules. Although

36 species of primitive spatangoids have been analysed, consideration of many more species is needed for a more detailed phylogenetic exploration within and among the clades in the Spatangoida.

REFERENCES

BENTON, M. J., HITCHIN, R. and WILLS, M. A. 1999. Assessing congruence between cladistic and stratigraphic data. *Systematic Biology*, **48**, 581–596.

BEURLEN, K. 1934. Monographie der Echinoiden Familie Collyritidae d'Orb. *Palaeontographica*, *A*, **80**, 41–194.

BRITO, I. M. and RAMIREZ, L. V. O. 1974. Contribuição ao Conhecimento dos Equinóides Albianos (Cretáceo inferior) do Brasil. *Anais da Academia Brasileira de Ciências*, **46**, 275–282.

CHECCHIA-RISPOLI, G. 1945. Di due nuovi generi di Echini del Cretaceo della Somalia. *Bollettino del'Ufficio Geologico d'Italia*, **68** (8), 81–90.

CHESHER, R. H. 1963. The morphology and function of the frontal ambulacrum of *Moira atropos* (Echinoidea: Spatangoida). *Bulletin of Marine Science in the Gulf and Caribbean*, **13**, 549–573.

COOKE, C. W. 1955. Some Cretaceous echinoids from the Americas. *United States Geological Survey, Professional Paper*, **264-E**, 87–112.

COQUAND, H. 1880. Etude supplémentaire sur la paléontologie algérienne faisant suite à la description géologique et paléontologique de la région sud de la province de Constantine. *Bulletin de l'Académie Hippone* (Bone), **15**, 449 pp.

DAVID, B. 1980. Un modèle d'ontogenèse: la croissance de *Toxaster granulosus kiliani* (Lambert), échinide spatangoïde du Valanginien. *Geobios*, **13**, 903–926.

—— 1988. Origins of the deep-sea holasteroid fauna. 331–346. *In* PAUL, C. R. C. and SMITH, A. B. (eds). *Echinoderm phylogeny and evolutionary biology*. Clarendon Press, Oxford, 373 pp.

—— 1993. How to study evolution in echinoderms. 1–80. *In* JANGOUX, M. and LAWRENCE, J. M. (eds). *Echinoderm studies*. Balkema, Rotterdam, 376 pp.

—— CHONÉ, T. de, RIDDER, C. and FESTEAU, A. 2000. Antarctic echinoids. An interactive database on CD-ROM. Biogéosciences Publisher, Université de Bourgogne. Version 1.0.

DEVRIÈS, A. 1955. Note sur le genre *Heteraster*. *Bulletin de la Société Géologique de France*, **6**, 315–323.

—— 1956. Sur une nouvelle espèce d'échinide en Algérie: *Enallaster transians*, Pomel. *Bulletin du Service de la Carte Géologique d'Algérie*, **8**, 251–267.

—— 1960*a*. Contribution à l'étude de quelques groupes d'échinides fossiles d'Algérie. *Publications du Service de la Carte Géologique d'Algérie*, **3**, 279 pp.

—— 1960*b*. Contribution à l'étude de l'ontogénie de quelques formes d'échinides fossiles. *Publications du Service de la Carte Géologique d'Algérie*, **5**, 56–103.

—— 1963. Intérêt stratigraphique des caractères chez les échinides Spatangoidea au Crétacé inférieur (et au Crétacé en général). *In* Colloque sur le Crétacé inférieur, Lyon. *Mémoires du Bureau de Recherche Géologiques et Minières*, **34**, 419–427.

—— 1973. Suite aux échinides d'Algérie. *Publications du Service de la Carte Géologique d'Algérie* (*Nouvelle Série*), **44**, 45–100.

DURHAM, J. W. 1966. Classification. 270–295. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*, *Part U*, *Echinodermata. Echinozoa-Echinoidea*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 695 pp.

—— and MELVILLE, R. V. 1957. A classification of echinoids. *Journal of Paleontology*, **31**, 242–272.

EBLE, G. J. 2000. Contrasting evolutionary flexibility in sister groups: disparity and diversity in Mesozoic atelostomate echinoids. *Paleobiology*, **26**, 56–79.

FISCHER, A. G. 1966. Order Spatangoida. 367–695. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*, *Part U*, *Echinodermata. Echinozoa-Echinoidea*. Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 695 pp.

GORDON, I. 1926. The development of the calcareous test of *Echinocardium cordatum*. *Philosophical Transactions of the Royal Society of London*, *B*, **215**, 255–313.

HENDY, M. D. and PENDY, D. 1982. Branch and bound algorithms to determine minimal evolutionary trees. *Mathematical Biosciences*, **59**, 277–299.

JABLONSKI, D. and BOTTJER, D. J. 1990. The origin and diversification of major groups: environmental patterns and

macroevolutionary lags. 17–57. *In* TAYLOR, P. D. and LARWOOD, G. P. (eds). *Major evolutionary radiations.* Systematics Association, Special Volume, **42**, Clarendon Press, Oxford, 437 pp.

JEFFERY, C. H. 1999. A reappraisal of the phylogenetic relationships of somaliasterid echinoids. *Palaeontology*, **42**, 1027–1041.

JENSEN, M. 1988. Functional morphology and systematics of Spatangoids (Euechinoidea). 327–335. *In* BURKE, R. D., MLADENOV, P. V., LAMBERT, P. and PARSLEY, R. L. (eds). *Echinoderm biology.* Balkema, Rotterdam, 832 pp.

KANAZAWA, K. 1992. Adaptation of test shape for burrowing and locomotion in spatangoid echinoids. *Palaeontology*, **35**, 733–750.

KIER, P. M. 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *Journal of Paleontology*, **48**, Supplement 3, 1–95.

—— 1984. Fossil spatangoid echinoids of Cuba. *Smithsonian Contributions to Paleobiology*, **55**, 336 pp.

LAMBERT, J. 1892. Etudes morphologiques sur le plastron des Spatanguidés. *Bulletin de la Société des Sciences Historique et Naturelle de l'Yonne*, **47**, 55–98.

—— 1895. Essai d'une monographie du genre *Micraster* et note sur quelques échinides. 149–167. *In* GROSSOUVRE, A. de. *Recherche sur la craie supérieure.* Mémoires du Service de la Carte Géologique de la France, **1**, 558 pp.

—— 1920*a*. Note sur quelques échinides du Crétacé inférieur de la Provence. *Notes Provençales*, **11**, 1–24.

—— 1920*b*. Etude sur quelques formes primitives de spatanguidés. *Bulletin de la Société des Sciences Historique et Naturelle de l'Yonne*, **5** (73), 1–23.

—— 1926. Considérations sur les échinides de la Commanche série du Texas. *Bulletin de la Société Géologique de France*, **4**, 263–278.

—— 1931. Etude sur les échinides du nord de l'Afrique. *Mémoires de la Société Géologique de France*, **16**, 5–108.

—— and THIÉRY, P. 1924. 385–512. *In: Essai de nomenclature raisonnée des échinides.* Librairie Septime Ferrière, Chaumont, Fasc. 6–7 (published in parts).

—— —— 1925. 513–607. *In: Essai de nomenclature raisonnée des échinides.* Librairie Septime Ferrière, Chaumont, Fasc. 8–9 (published in parts).

LOBACHEVA, S. 1968. On the Early Cretaceous sea urchins of the genus *Epiaster* from Turkmenistan. *Annual Review of the Soviet Paleontological Society*, **18**, 268–281. [In Russian].

LOVÉN, S. 1874. Etudes sur les échinoïdes. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, **11** (7), 91 pp.

MADON-SENEZ, C. 1998. Disparité morphologique et architecturale des Schizasteridae incubants (Echinoidea, Spatangoida) des régions australes. Thèse de l'Université de Bourgogne, inédit, 262 pp.

MASROUR, M. 1987. Etude des échinides du Crétacé inférieur de la région de Tarhazoute (Haut Atlas occidental, Maroc). Thèse de 3ème cycle, Université Claude Bernard, Lyon, inédit, 135 pp.

MCNAMARA, K. J. 1985. Taxonomy and evolution of the Cainozoic spatangoid echinoid *Protenaster*. *Palaeontology*, **28**, 311–330.

—— 1987. Taxonomy, evolution and functional morphology of southern Australian Tertiary hemiasterid echinoids. *Palaeontology*, **30**, 44–48.

MESPOULHÉ, P. 1992. Morphologie d'un échinide irrégulier subantarctique de l'archipel des Kerguelen: ontogenèse, dimorphisme sexuel et variabilité. Thèse de l'Université de Bourgogne, inédit, 185 pp.

MINTZ, L. W. 1966. The origins, phylogeny, descendants of the echinoid family Disasteridae, A. Gras, 1848. Unpublished PhD thesis, University of California, Berkeley, 314 pp.

—— 1968. Echinoids of the Mesozoic families Collyritidae d'Orbigny, 1853 and Disasteridae Gras, 1848. *Journal of Paleontology*, **42**, 1272–1288.

MOOI, R. and DAVID, B. 1996. Phylogenetic analysis of extreme morphologies: deep-sea holasteroid echinoids. *Journal of Natural History*, **30**, 913–953.

—— MARTINEZ, S. and PARMA, S. G. 2000. Phylogenetic systematics of Tertiary monophorasterid sand dollars (Clypeasteroida: Echinoidea) from South America. *Journal of Paleontology*, **74**, 263–281.

MORTENSEN, T. 1907. Echinoidea. *Danish Ingolf Expedition*. Bianco Luno, Copenhagen, **4** (2), 200 pp. (published in parts).

—— 1950. *A monograph of the Echinoidea. V.1. Spatangoida.* Reitzel C. A., Copenhagen, 432 pp.

—— 1951. *A monograph of the Echinoidea. V.2. Spatangoida.* Reitzel C. A., Copenhagen, 593 pp.

MOUSSA, B. 1999. Biometrics analysis of variation in spatangoid echinoid *Linthia* from the Maastrichtian and Paleocene of the Iullemmenden Basin, Niger, West Africa. 341–346. *In* CANDIA CARNEVALI, D. and BONASORO, F. (eds). *Echinoderm Research 1998.* Balkema, Rotterdam, 580 pp.

—— 2001. Echinofaunes maastrichtiennes et paléocènes du Bassin des Iullemmenden (Niger occidental). Quantification de la disparité morphologique chez *Linthia* (Echinoidea, Spatangoida). Thèse de l'Université de Bourgogne, inédit, 440 pp.

NÉRAUDEAU, D. 1990. Ontogenèse, paléoécologie et histoire des *Hemiaster*, échinides irréguliers du Crétacé. Thèse de l'Université de Bourgogne, inédit, 194 pp.

—— 1991. Influence du jeu de transgressions-regressions sur les chronomorphoclines d'échinides et leurs inter-prétations phylogénétiques. *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, **313**, 717–722.

—— 1992. Transgressions-regressions and echinoid morphoclines. *Lethaia*, **25**, 219–220.

—— 1994*a*. Main stages of diversification in hemiasterid echinoids and closely related spatangoids. 809–811. *In* DAVID, B., GUILLE, A., FÉRAL, J.-P. and ROUX, M. (eds). *Echinoderms through time*. Balkema, Rotterdam, 992 pp.

—— 1994*b*. Hemiasterid echinoids (Echinodermata: Spatangoida) from the Cretaceous Tethys to the present-day Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **110**, 319–344.

—— 1995. Diversité des échinides fossiles et reconstitutions paléoenvironnementales. *Geobios, Mémoire Spécial*, **18**, 337–345.

—— and BRETON, G. 1993. Un assemblage de *Macraster* cf. *polygonus*, spatangoide primitif de l'Albien moyen de Saint-Jouin (Seine-Maritime): developpement ontogénique, démographie, paléoécologie. *Bulletin Trimestriel de la Société Géologique de Normandie et Amis du Muséum du Havre*, **80** (3–4), 53–62.

—— and FLOQUET, M. 1991. Les échinides Hemiasteridae: marqueurs écologiques de la plate-forme castillane et navarro-cantabre (Espagne) au Crétacé supérieur. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **88**, 265–281.

—— and MATHEY, B. 2000. Biogeography and diversity of the South Atlantic Cretaceous echinoids: implications for circulation patterns. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **156**, 71–88.

—— and MOREAU, P. 1989. Paléoécologie et paléobiogéographie des faunes d'échinides du Cénomanien nord-aquitain (Charente-Maritime, France). *Geobios*, **22**, 293–324.

—— DAVID, B. and AL-MUALLEM, M. S. 1995. The Cretaceous echinoids from the central Saudi Arabia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **197**, 399–424.

—— —— and MADON, C. 1998. Tuberculation in spatangoid fascioles: delineating plausible homologies. *Lethaia*, **31**, 323–334.

NEUMANN, C. 1999. New spatangoid echinoids (Echinodermata) from the Upper Cretaceous of Jordan: their taxonomy and phylogenetic importance. *Berliner Geowissenschaftliche Abhandlung, E*, **30**, 175–189.

ORBIGNY, A. d' 1853–55. *Paléontologie Française. Description zoologique et géologique de tous les animaux mollusques et rayonnés fossiles de France. Echinides irréguliers. Terrains crétacés*. Masson, Paris, **6**, 596 pp.

POMEL, A. 1883. *Classification méthodique des genres d'échinides vivants et fossiles*. Jourdan, Alger, 1–120.

REY, J. 1972. Recherches géologiques sur le Crétacé inférieur de l'Estremadura (Portugal). *Mémoires du Service Géologique du Portugal*, **21**, 477 pp.

RIDDER, C. de and LAWRENCE, J. M. 1982. Food and feeding mechanisms: Echinoidea. 57–115. *In* JANGOUX, M. and LAWRENCE, J. M. (eds). *Echinoderm nutrition*. Balkema, Rotterdam, 700 pp.

ROEMER, F. 1888. *Macraster* eine neue Spatangoiden Gattung aus der Kreide von Texas. *Neues Jahrbuch für Geologie und Paleontologie*, **1**, 191–195.

SAVIN, L. 1903. Catalogue raisonné des échinides fossiles du département de la Savoie. *Bulletin de la Société d'Histoire Naturelle de Savoie*, **2**, 109–315.

SMITH, A. B. 1980*a*. The structure and arrangement of echinoid tubercles. *Philosophical Transactions of the Royal Society of London, B*, **289**, 1–54.

—— 1980*b*. The structure, function and evolution of tube feet and ambulacral pores in irregular echinoids. *Palaeontology*, **23**, 39–84.

—— 1981. Implications of lantern morphology for the phylogeny of post-Palaeozoic echinoids. *Palaeontology*, **24**, 779–801.

—— 1984. *Echinoid palaeobiology*. Allen and Unwin, London, 190 pp.

—— 1988. Echinoids. 16–189. *In* SMITH, A. B., PAUL, C. R. C., GALE, A. S. and DONOVAN, S. K. *Cenomanian and lower Turonian echinoderms from Wilmington, south-east England*. Bulletin of the British Museum (Natural History), Geology, **42**, 241 pp.

—— and JEFFERY, C. H. 2000. Maastrichtian and Paleocene echinoids: a key to world fauna. *Special Papers in Palaeontology*, **64**, 406 pp.

—— and WRIGHT, C. W. 1989. British Cretaceous echinoids. Part 1. General introduction and Cidaroida. *Monograph of the Palaeontographical Society of London*, **578**, 1–100.

—— —— 1990. British Cretaceous echinoids. Part 2, Echinothuroida, Diadematoida and Stirodonta. *Monograph of the Palaeontographical Society of London*, **578**, 101–198.

—— SIMONS, M. D. and RACEY, A. 1990. Cenomanian echinoids, larger foraminifera and calcareous algae from the Natih Formation, Central Oman Mountains. *Cretaceous Research*, **11**, 29–69.

SOLOVJEV, A. N. 1989. New echinoid genus *Eoholaster* (Spatangoida, Holasteroidae) from the Berriasian. 148–155. *In*

KALO, D. L., ROJNOV, C. W., SOLOVJEV, A. N., STUKALINA, G. A. and XINTS, L. M. (eds). *Fossil and Recent echinoderm researches*. Academy of Sciences of the Estonian SSR, Tallinn, 224 pp. [In Russian].

—— and MARKOV, A. V. 1999. Fossil pericosmid echinoids. 399–404. *In* CANDIA CARNEVALI, D. and BONASORO, F. (eds). *Echinoderm research 1998*. Balkema, Rotterdam, 580 pp.

STOKES, R. B. 1977. The echinoids *Micraster* and *Epiaster* from the Turonian and Senonian chalk of England. *Palaeontology*, **20**, 106–109.

SWOFFORD, D. L. 1993. PAUP, Phylogenetic Analysis Using Parsimony, version 3·1·1. Copyright Smithsonian Institution.

VILLALBA–CURRAS, M. P. 1993. *Revision de los equinoideos del Cretacico inferior y medio espanol*. Universidad Complutense de Madrid, 568 pp.

VILLIER, L., DAVID, B. and NÉRAUDEAU, D. 2001. Ontogenetic and morphological evolution of the ambulacral pores in *Heteraster* (early spatangoids). 563–567. *In* BARKER M. (ed.). *Echinoderm 2000*. Balkema, Rotterdam, 612 pp.

WILLS, M. A. 1999*a*. Congruence between phylogeny and stratigraphy: randomization test and the gap excess ratio. *Systematic Biology*, **48**, 559–580.

—— 1999*b*. GHOSTS 2.4. Significance tests for RCI, SCI and GER values by randomization. Basic code for chipmunk-basic 3.5.3.

ZAGHBIB-TURKI, D. 1987. Les échinides du Crétacé de Tunisie. Paléoécologie générale: systématique, paléoécologie, paléobiogéographie. Thèse de la faculté des Sciences de Tunis, inédit, 609 pp.

—— 1989. Les échinides indicateurs des paléoenvironnements: un exemple dans le Cénomanien de Tunisie. *Annales de Paléontologie (Invertébrés)*, **75**, 63–81.

LOÏC VILLIER

Université de Provence
Centre de Sédimentologie-Paléontologie
Bâtiment de Sciences Naturelles
Place Victor Hugo
Case 67
13 331 Marseille cedex 03, France
e-mail lvillier@up.univ-mrs.fr

DIDIER NÉRAUDEAU

Université de Rennes
UMR CNRS 6118: Géosciences
Campus de Beaulieu
163 av. du Général Leclerc
35042 Rennes cedex, France
e-mail didier.neraudeau@univ-rennes1.fr

BERNARD CLAVEL

Les Repingons
74140 Messery, France
e-mail b.clavel@wanadoo.fr

CHRISTIAN NEUMANN

Humboldt Universität zu Berlin
Museum für Naturkunde – Institut für Paläontologie
Invalidenstrasse 43
10115 Berlin, Germany
e-mail Christian.Neumann@MUSEUM.HU-Berlin.de

BRUNO DAVID

Université de Bourgogne
UMR CNRS 5561: Biogéosciences
Centre des Sciences de la Terre
6, Bd. Gabriel
21000 Dijon, France
e-mail bruno.david@u-bourgogne.fr

APPENDIX

List of species used in the cladistic analysis

Thirty-six species were included in the cladistic analysis but nearly 150 were taken into account during the character analysis.

Taxon	Stratigraphic range	Collection
Disaster elongatus d'Orbigny	Valanginian	David, University of Burgundy
'*Toxaster*' *laffittei* Devriès	Berriasian	Devriès, University of Poitiers
Aphelaster integer (Gauthier)	Valanginian	David, University of Burgundy
Douvillaster longesulcatus (Cotteau, Peron and Gauthier)	Albian	Cotteau, University of Lyon
Douvillaster vatonnei (Coquand)	Albian–Cenonanian	Lambert, MNHN, Paris
Epiaster henricii Cotteau	Cenomanian	Devriès, University of Poitiers
Epiaster maximus Coquand	Cenomanian	Devriès, University of Poitiers
Epiaster restrictus Gauthier	Aptian	Devriès, University of Poitiers
Hemiaster dallonii Lambert	Cenomanian	Ciry, University of Burgundy
Hemiaster zululandensis Besairie and Lambert	Albian	Lambert, MNHN, Paris
Heteraster corvensis (de Loriol)	Hauterivian	Rey, University of Toulouse
Heteraster oblongus (Brongniart)	Barremian–Aptian	Rey, University of Toulouse
Heteraster renevieri (Desor)	Aptian–Albian	Rey, University of Toulouse
Heteraster texanus (Roemer)	Albian	Devriès, University of Poitiers
Heteraster transians (Devriès)	Albian	Devriès, University of Poitiers
Macraster besairiei (Lambert)	Albian	Collignon, University of Burgundy
Macraster elegans (Adkins)	Albian	Lambert, MNHN, Paris
Macraster polygonus (d'Orbigny)	Aptian–Albian	Seunes, University of Rennes
Mecaster batnensis (Coquand)	Cenomanian	Lambert, MNHN, Paris
Micraster distinctus Agassiz	Cenomanian	Néraudeau, University of Rennes
Micraster michelini Agassiz	Cenomanian	David, University of Burgundy
Palhemiaster comanchei (Clark)	Albien	Néraudeau, University of Rennes
Palhemiaster peroni Lambert	Aptian–Albian	Devriès, University of Poitiers
Periaster elatus (Desmoulins)	Cenomanian	Néraudeau, University of Rennes
Periaster undulatus d'Orbigny	Cenomanian	Néraudeau, University of Rennes
Polydesmaster fourtaui Lambert	Cenomanian	Lambert, MNHN, Paris
Toxaster collegnoi (Sismonda)	Aptian	Devriès, University of Poitiers
Toxaster granosus d'Orbigny	Valanginian	David, University of Burgundy
Toxaster maurus Lambert	Haut.-Barremian	David, University of Burgundy
Toxaster peroni Lambert	Hauterivian	David, University of Burgundy
Toxaster radula Gauthier	Albian	Lambert, MNHN Paris
Toxaster retusus (Lamarck)	Hauterivian	David, University of Burgundy
Toxaster rochi Coquand	Berriasian	Devriès, University of Poitiers
Toxaster seynenis Lambert	Barremian	David, University of Burgundy
Toxaster villei Gauthier	Barremian–Aptian	Devriès, University of Poitiers
Washitaster riovistae (Adkins)	Albian	Devriès, University of Poitiers

Data matrix analysed to produce tree in Text-figure 9

```
Disaster elongatus        00000   00000   00000   00000   0030?   00000   000?0
'Toxaster' laffittei      00000   00000   00000   00000   00000   00000   00000
Aphelaster integer        00000   01000   00100   21111   00011   00000   00000
Toxaster rochi            00000   01000   00100   21111   00010   00000   00000
Toxaster granosus         00100   01100   00101   11111   00010   00000   11000
Toxaster retusus          00110   11101   00111   11110   00112   00000   11110
Toxaster villei           00110   21221   20121   12211   00121   10010   11100
Toxaster peroni           00110   21222   20220   12211   00111   10010   11100
Toxaster maurus           001?0   21121   10110   12211   00111   10010   11100
Toxaster seynensis        00110   11121   20111   12110   00112   10010   11111
Toxaster collegnoi        00110   21121   20111   12200   00112   10010   11111
Toxaster radula           00110   21122   20211   12110   00111   10011   11100
Heteraster corvensis      00110   11111   10111   11110   11121   00000   11110
Heteraster oblongus       00110   21111   10111   01110   11121   00000   11110
Heteraster renevieri      00110   21121   20111   11210   11122   00000   10110
Heteraster texanus        01110   21121   20111   01310   11222   00100   11110
Heteraster transiens      00010   21222   21220   22220   11221   10010   11100
Washitaster riovistae     01110   31121   20111   01310   11223   10100   12110
Micraster distinctus      00111   11222   20212   12200   00112   10121   11201
Micraster michelini       00011   11222   20212   12200   00112   22221   11101
Macraster polygonus       00110   11222   20212   12210   00112   10011   11100
Macraster elegans         00010   11222   20221   22210   00212   10110   11100
Douvillaster vattonei     00010   11222   21221   22220   00212   10120   12100
D. longesulcatus          000?0   11222   21220   22220   00211   10110   11100
Epiaster maximus          00010   21222   20221   22210   00211   10110   1210?
Epiaster besairiei        00010   11222   20221   22220   00212   10110   12100
Epiaster henricii         00110   21223   30221   22200   00211   11121   11101
Epiaster restrictus       00110   21223   30222   12200   00211   12120   11201
Palhemiaster peroni       00110   31223   30221   12200   00111   10021   11100
Palhemiaster comanchei    00110   21222   20211   12200   00212   11010   11101
Mecaster batnensis        01100   01223   30221   22200   00221   11121   12101
Periaster undulatus       00110   31223   30221   12200   00121   22121   11201
Periaster elatus          00110   31223   30221   12200   00122   22221   10211
Hemiaster dallonii        10100   01223   30210   12200   00211   20110   11101
Hemiaster zululandensis   101?0   21223   30211   12200   00211   20010   1110?
Polydesmaster fourteaui   001?0   31223   30201   12200   00?21   12121   22101
```