IMPLICATIONS OF LANTERN MORPHOLOGY FOR THE PHYLOGENY OF POST-PALAEOZOIC ECHINOIDS

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ABSTRACT. Aristotle's lanterns of the Liassic echinoids *Diademopsis tomesii* (Wright) and *Eodiadema* aff. *minutum* (Buckman) are described, and compared with those of living echinoids. *Diademopsis* has a primitive lantern and weakly grooved teeth. The ultrastructure of these teeth is well preserved, and it is shown how Recent grooved, keeled, and diamond-shaped teeth could be derived from a tooth of this construction. *Eodiadema* has diamond-shape teeth of a type previously known only in irregular echinoids, and its lantern is intermediate in form between the regular *Diademopsis*-type of lantern and two types of irregular echinoid lantern (cassiduloid and holectypoid).

The evolution of tooth and lantern in post-Palaeozoic echinoids is outlined, and is the basis for constructing a phylogeny. All living echinoids form a monophyletic group whose stem-group includes archaeocidarids and some miocidarids as its most advanced members. Cidarids are the monophyletic primitive sister group to the euechinoids and, within the Euechinoidea, echinothurioids are the primitive sister group to all others. Irregular echinoids are a monophyletic group with a stem group that includes *Eodiadema* as one of its members. Irregular echinoids are separated into three groups, eognathostomates, neognathostomates, and atelostomates. Eognathostomates, comprising pygasteroids and holectypoids, are the primitive sister group of all other irregular echinoids. Cassiduloids and clypeasteroids are grouped together as neognathostomates while spatangoids and holasteroids are placed in the atelostomates. Echinaceans are another monophyletic group whose most primitive members belong to the Pseudodiadematidae. Echinaceans and irregulars both evolved from an aulodont ancestor.

SINCE the classic work of Jackson (1912) on the Aristotle's lantern of living and fossil echinoids, the morphology of this structurally complex gripping apparatus has been of importance in unravelling the phylogeny of the Echinoidea. The lantern of fossil echinoids is rarely preserved as it rapidly dissociates and disintegrates after death. Kier (1977) could fined less than fifteen Triassic or Jurassic species of echinoid where the lantern was know. This is a lamentably poor record for the period during which the great majority of echinoid orders evolved.Relatively little is known about the early evolution of the Aristotle's lantern in euechinoids and previous workers have had to rely heavily on interpreting the comparative morphology of lanterns in living echinoids.

This paper describes, for the first time, lantern elements of two Lower Liassic echinoids, *Diademopsis tomesii* (Wright) and *Eodiadema* aff. *minutum* (Buckman). These two genera occupy a significant position in the evolution of euechinoids as *Eodiadema* is the earliest supposed diadematoid and *Diademopsis* is one of only two genera of pedinoid reported from the Triassic. Recent work on the lanterns of living echinoids by Märkel (1969, 1970*a*, *b*, *c*, 1974, 1978, 1979) and Jensen (1974, 1979), has added greatly to our understanding of this apparatus. However, Märkel and Jensen have come to somewhat different conclusions concerning the phylogeny of echinoids. A cladistic approach to echinoid phylogeny, as attempted by Märkel (1970*a*), can only succeed by using characteristics known to be synapomorphic, preferably from fossil evidence. The detailed structure of these Liassic lanterns is therefore of some importance.

METHODS AND MATERIALS

Partially dissociated tests and isolated elements of *Diademopsis tomesii* (Wright) were collected from a finely laminated shale approximately two feet above the base of the Lias in the lower part of the *pre-planorbis* zone (Hettangian: bed 31 of Hallam, 1956). Most of the material was collected at Tolcis Quarry near Axminster, Dorset but specimens were also collected at Pinhay Bay, Lyme Regis, Dorset. Tests of *D. tomesii* are not uncommon but have usually collapsed and partially dissociated. Spines litter many of the bedding planes. No evidence of any other species of echinoid was found at this horizon.

Shale samples with partially dissociated tests and isolated elements of *Eodiadema aff. minutum* (Buckman) were kindly supplied by Dr. R. A. Hewitt. These were collected from the upper part of the *ibex* zone, Lower Pliensbachian (bed D of Hewitt and Hurst, 1977) at Blockley Quarry, Gloucestershire. They are identical to specimens from the Green Ammonite Beds (Lower Pliensbachian) at Lyme Regis, Dorset. This species has compound ambulacra with an enlarged tubercle on every third plate. Each interambulacral plate has a single large primary tubercle that is perforate and crenulate. The areoles are confluent, at least near the ambitus. It differs from *Eodiadema minutum* in having denser secondary tuberculation on interambulacral plates. *Eodiadema* is tolerably abundant at this horizon in Blockley Quarry and its spines are particularly common. In thorough quantitative sampling of this section, the only other echinoid fragments to come from this horizon were three cidarid spines (Hewitt, pers. comm.). No evidence was found in this bed of any other euechinoid.

Individual skeletal elements were loosened by applying a solution of detergent with a soft-haired brush and then cleaned by ultrasonic vibrator in a 50 : 50 solution of detergent and water. Elements were gently etched in a 0·1 N solution of formic acid for a couple of minutes in order to develop the stereom. Finally they were mounted and gold coated for the scanning electron microscope. All material is deposited in the British Museum (Natural History), London.

THE LANTERN OF *DIADEMOPSIS TOMESII*

Teeth (text-figs. 1 and 2)

Individual teeth are broad, weakly grooved and moderately straight, at least distally. The tooth comes to a V-shaped point ventrally. There is a broad abaxial ridge divided by a median groove. The axial face has a weak groove and in cross-section the tooth is crescentic. Each tooth (text-fig. 2a–c) is composed of a double column of primary plates with small secondary plates and central and lateral prism zones. Primary tooth plates have only a shallow corner between their broad median section and tapering lateral section and correspond to the echinothuriid-type of Jensen (1979). Secondary plates are best developed laterally where they are very prominent. There is a major zone of prisms near the centre of the axial face and two small zones of prisms at the lateral edges. The adaxial face of the tooth is thus composed of lateral ridges, where steeply inclined secondary plates can be seen, and a central, gently concave area of prisms (text-fig. 2i, j).

In over-all shape, these teeth closely resemble the teeth of Palaeozoic archaeocidarids and they are also very similar to teeth of echinothurioids (see Märkel, 1970a, Jensen, 1979). Teeth of Recent pedinoids have not yet been described in detail but those of diadematoids are more U-shaped in cross-section (Märkel, 1970a) and, in this respect, resemble teeth of living cidaroids (Märkel and Titschack, 1969). The teeth of *Diademopsis* have a structure similar to those of living diadematoids and echinothurioids except that, in *Diademopsis*, secondary plates are more strongly developed while the central prism zone is conversely rather less well developed (see text-fig. 5).

Demi-pyramids (text-figs. 1 and 2d, e)

The foramen magnum is a large, V-shaped notch extending approximately half way down the pyramid. It is relatively broad and more or less straight-edged. From each demi-pyramid there extends a triangular processus superioris. No processus supra alveolaris is developed from the

processus superioris, nor do styloid processes extend into the foramen magnum (compare with Recent diadematoids, text-fig. 6F). The abaxial face has a prominent ridge by the intrapyramidal suture and a deep wedge-shaped depression laterally. The lateral wing is large and triangular with a flat dorsal edge. It is covered in many fine horizontal ridges that are slightly sinuous and these extend beyond the wing forming a short comb-like fringe. The ventral tip of the demi-pyramid is strongly curved axially to enclose the tooth and there is a weakly developed tooth clamp. The surface of the intrapyramidal suture is narrow and gently curved. There is a dental slide on the axial face and a single, large, deep pit lateral to the processus superioris on the dorsal surface.
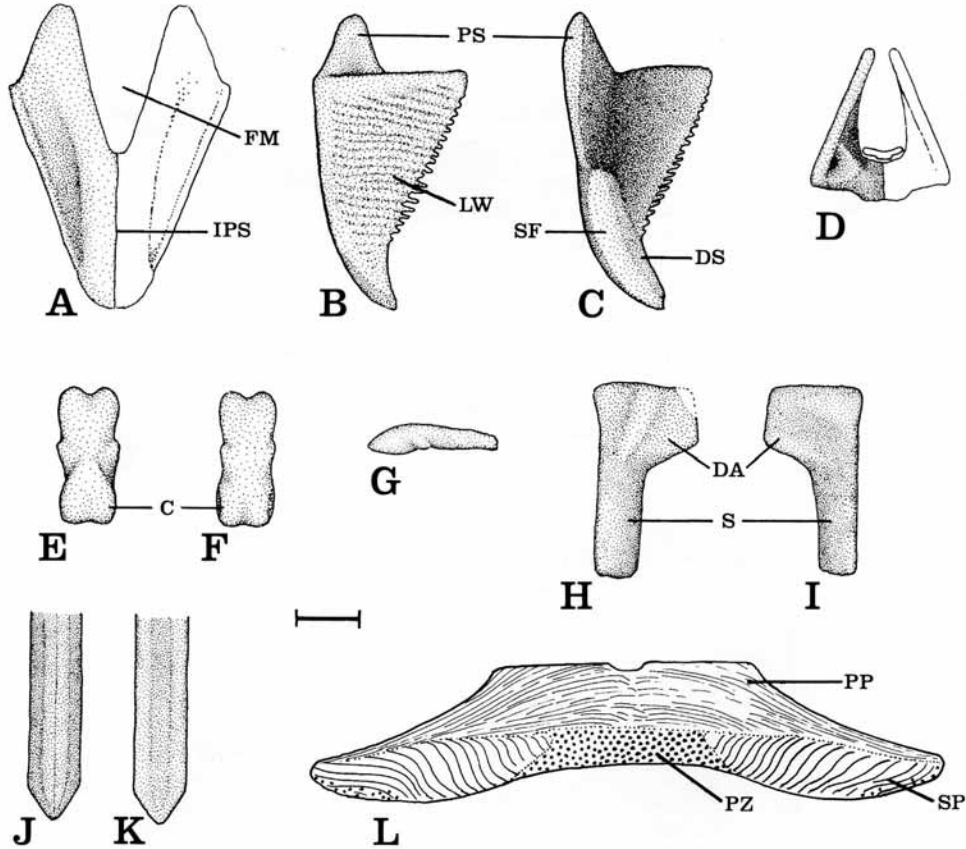
TEXT-FIG. 1. Lantern elements of *Diademopsis tomesii* (Wright). A–D. Demi-pyramids: A, abaxial face (right-hand side element reconstructed in outline to show shape of the pyramids); B, interpyramidal face; C, intrapyramidal face; D, dorsal (reconstructed as in A, tooth outline also reconstructed.) E–G. Rotula: E, dorsal; F, ventral; G, lateral. H, I, epiphysis: H, interpyramidal face; I, intrapyramidal face. J–L, tooth: J, abaxial face; K, adaxial face; L, cross-section.

Scale bar for figs. A–K = 1 mm, all camera lucida drawings. L based on S.E.M. micrographs, not to scale. C—condylus, DA—demi-arc, DS—dental slide, FM—foramen magnum, IPS—intrapyramidal suture, LW—lateral wing, PP—primary tooth plate, PS—processus superioris, PZ—prism zone, SF—suture face, S—shaft, SP—secondary tooth plate.

The deep, straight-edged foramen magnum, the dorsal pitting and the comb-like fringe to the lateral wing are all features typical of euechinoid demi-pyramids. These features are not present in archaeocidarids and cidarids. However, the demi-pyramids of *Diademopsis*, though clearly corresponding to the euechinoid type, are rather peculiar in that the processus superioris appears to lack a processus supra alveolaris. In stirodonts and most aulodonts, the processus supra alveolaris is well developed and helps to support the tooth. The phormosomid echinothurioids are the only group
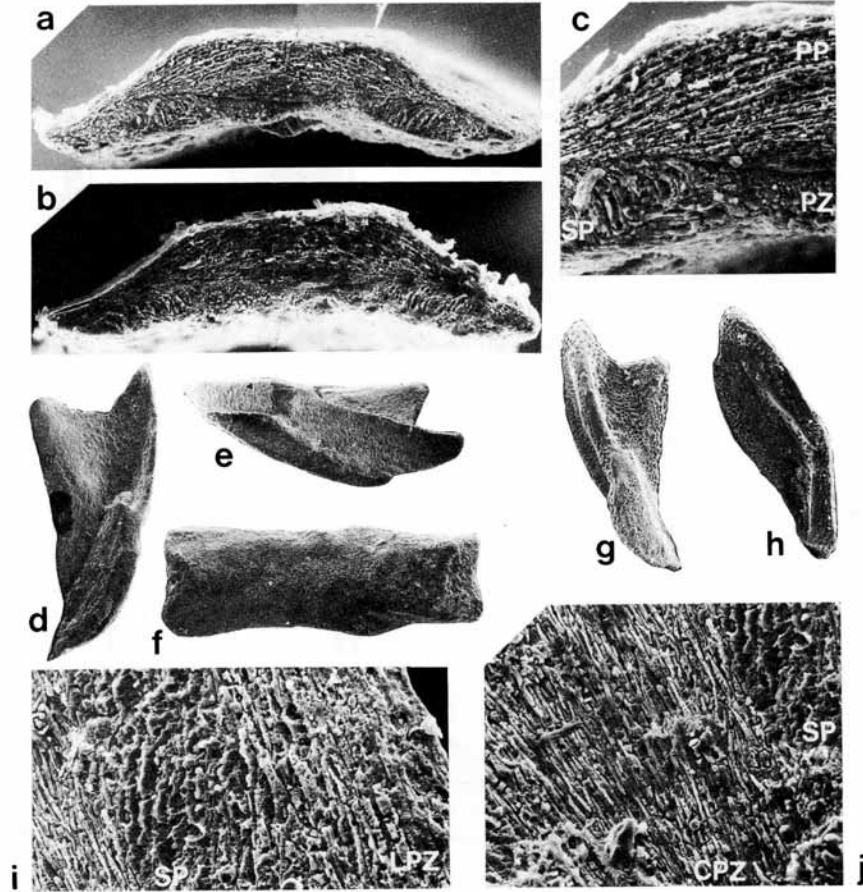
TEXT-FIG. 2. *a–f, i, j*, lantern of *Diademopsis tomesii* (Wright) (BMNH E76884/5). *a*. Cross-section of a tooth, abaxial face to the top, × 105. *b*. Cross-section of another tooth near the ventral point, × 110. *c*. Enlargement of tooth cross-section seen in *a*, × 240. *d*. Demi-pyramid, intrapyramidal face, × 11. *e*. Demi-pyramid, abaxial face (adoral point to left: viewed slightly obliquely), × 11. *f*. Rotula, dorsal face, × 25. *g, h*, Demi-pyramids of *Eodiadema* aff. *minutum* (Buckman) (BMNH E 76886. *g*, Intrapyramidal face, × 30. *h*. Abaxial face, × 30. *i, j*. Tooth of *Diademopsis tomesii* (Wright). *i*. Axial face showing secondary plates and lateral prism zone, × 200. *j*. Axial face showing central prism zone, × 200. CPZ—central prism zone, LPZ—lateral prism zone, PP—primary plates, SP—secondary plates.

of aulodont euechinoids to lack this process. The demi-pyramids of camarodonts lack a processus supra alveolaris, their teeth being supported by specialized epiphyses, and demi-pyramids in holectypoids and the cassiduloid *Echinolampas* also lack a processus supra alveolaris.

The demi-pyramids of *Diademopsis bowerbanki* (Wright) (Sinemurian, Lower Liassic) were described by Hawkins (1934). In his illustration (loc. cit. fig. 9), the foramen magnum is shown as a deep slit and processi superioris are absent. I have re-examined Hawkins' specimen (BMNH E75360) and found the pyramid to be partially covered by sediment and the dorsal part hidden beneath the edge of the test. From what can be seen in this and in other specimens, the lantern of *Diademopsis bowerbanki* appears, in fact, to be very similar to the lantern of *D. tomesii* described here.

Epiphyses (text-fig. 1)

The epiphysis is a flat, axe-shaped plate with a relatively long shaft and a broad abaxial demi-arc. The lateral (interpyramidal) edge is more or less straight. On the opposite edge, the angle between the shaft and the demi-arc is obtuse. The ventral face of the demi-arc is slightly depressed centrally and the shaft has a weak ridge. The dorsal face of the demi-arc has a prominent ridge (crista) set at a slight angle to the shaft and this face of the shaft is relatively smooth. The intrapyramidal edge of the demi-arc is straight but slightly oblique to the shaft. Unlike a camarodont epiphysis, it is not sutured nor does it have any process for supporting the tooth. In life, the epiphyses would not have extended much into the foramen magnum (text-fig. 6E).

The epiphyses of *Diademopsis* are not like those of Recent diadematoids where the demi-arc is a narrower process that extends along the processus supra alveolaris (Jackson, 1912). Recent echinothurioids are mostly like Recent diadematoids in this respect except that in *Phormosoma* the demi-arc is absent or almost so. The epiphyses of camarodonts are sutured together interradially and have an additional projection for supporting the tooth. Both cidaroid and stirodont epiphyses have prominent demi-arcs, but those of *Eucidaris* have a deep glenoid cavity not present in *Diademopsis* (see Märkel, 1979). Stirodont epiphyses most closely resemble those of *Diademopsis*.

Rotulae (text-figs 1 and 2f)

Rotulae are dorso-ventrally flattened, roughly rectangular in outline and more or less parallel-sided. At the abaxial end there is a bifid condyle and close to this a pair of small, oblique ridges. Axially, the dorsal face of the rotula is divided by a weak median depression. Both inner and middle fossae are present.

The rotulae of *Diademopsis* conform in every detail with the rotulae of Recent euechinoids and belong to the 'hinge-joint' system described by Märkel (1979). This also appears to be the type of rotula found in Palaeozoic echinoids (Märkel, 1979; pers. obs.).

Compasses

Although compasses were seen, they proved too fragile to prepare for the S.E.M. They are long, narrow, flattened rods that taper axially and are bilobed abaxially. There appeared to be a slight symmetrical swelling about mid-length. There is nothing unusual about the compasses of *Diademopsis*.

Comparison with other lanterns

The lantern of *Diademopsis tomesii* shows a mixture of primitive and advanced characteristics and does not compare closely with any of the types of lantern described in Recent echinoids. The lantern is upright rather than oblique and is relatively narrow, unlike the lanterns of archaeocidarids and echinothurioids. The teeth are primitive in their structure, resembling those of archaeocidarids and echinothurioids but differing from the teeth of living cidarids and diadematoids. Pyramids have the deep foramen magnum and the dorsal pitting typical of euechinoids but the absence of processi supra alveolaris is a feature found among euechinoids only in some echinothurioid, camarodont and irregular echinoid lanterns. The lack of styloid processes is also unusual and occurs only in irregular echinoid groups and some echinothurioids. Epiphyses compare closest to those of stirodonts.

Rotulae show that the lantern, like that of living euechinoids, was hinge-jointed rather than socket-jointed.

The lantern of *Diademopsis* has clearly evolved somewhat from the archaeocidarid type of lantern and possesses several new features. Lanterns of living aulodonts, stirodonts and camarodonts all differ from it in some respects and each has evolved its own set of advanced characteristics not shared with the more primitive *Diademopsis* lantern.

THE LANTERN OF *EODIADEMA AFF. MINUTUM*

Teeth (text-figs. 3 and 4*b–f*)

The teeth are extremely small and noticeably curved, with a convex abaxial edge. They have a gently curved abaxial platform and are rhombic in cross-section. The lateral edges are developed as weak ridges. The two axial faces are very slightly concave and meet at a blunt axial edge. Lateral plates are clearly seen running obliquely across both axial faces. On abaxial faces, the primary plates are less oblique and in places are still covered by a fine retiform layer of stereom.

The fine structure is well preserved. Primary plates are small and restricted to the abaxial edge. Large triangular lateral plates are well developed and make up much of the tooth. Primary and lateral plates are paired and pairs of lateral plates overlap very slightly along much of their length. The prism zone is small and restricted to a central area just adaxial to the primary plates. Preservation is so good that even the basal lamella of the prism zone can be seen (text-fig. 2*c*).

This tooth is very like that found in juveniles of the Recent cassiduloid *Echinolampas* as described by Märkel (1978) and more or less identical but less well-preserved teeth of an unknown echinoid have been described from the Lower Pliensbachian (Liassic) by Märkel (1978).

Demi-pyramids (text-figs. 2*g*, *h*, and 3)

One extremely well-preserved demi-pyramid was found. This is small, and curves strongly towards the axis near its ventral point. The foramen magnum is relatively deep and broadens rapidly upwards (dorsally). There is a distinct processus superioris but no processus supra alveolaris. The lateral wing is triangular in shape and lacks the horizontal ridges seen in *Diademopsis*. The axial face has a clear dental slide but lacks styloid processes. The ventral tip is strongly curved to enclose the tooth. The abaxial face is broad and the pyramid roughly heart-shaped in outline. A thickened ridge of dense stereom runs from the processus superioris to the intrapyramidal suture. The dorsal surface lacks pits although stereom pores are larger here than elsewhere.
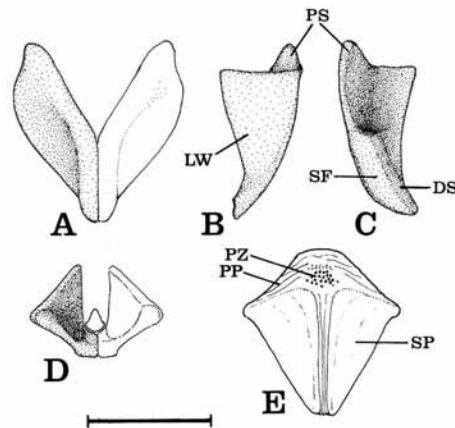
TEXT-FIG. 3. Lantern elements of *Eodiadema* aff *minutum* (Buckman). A–D. Demi-pyramids: A, abaxial face (right-hand side element reconstructed in outline to show the shape of the pyramids); B, interpyramidal face; C, intrapyramidal face; D, dorsal (reconstructed as in A, tooth also reconstructed). E. Cross-section of tooth.

Scale bar for figs. A–D = 1 mm, all camera lucida drawings. E based on S.E.M. micrographs and not to scale. Abbreviations as in text-fig. 1.
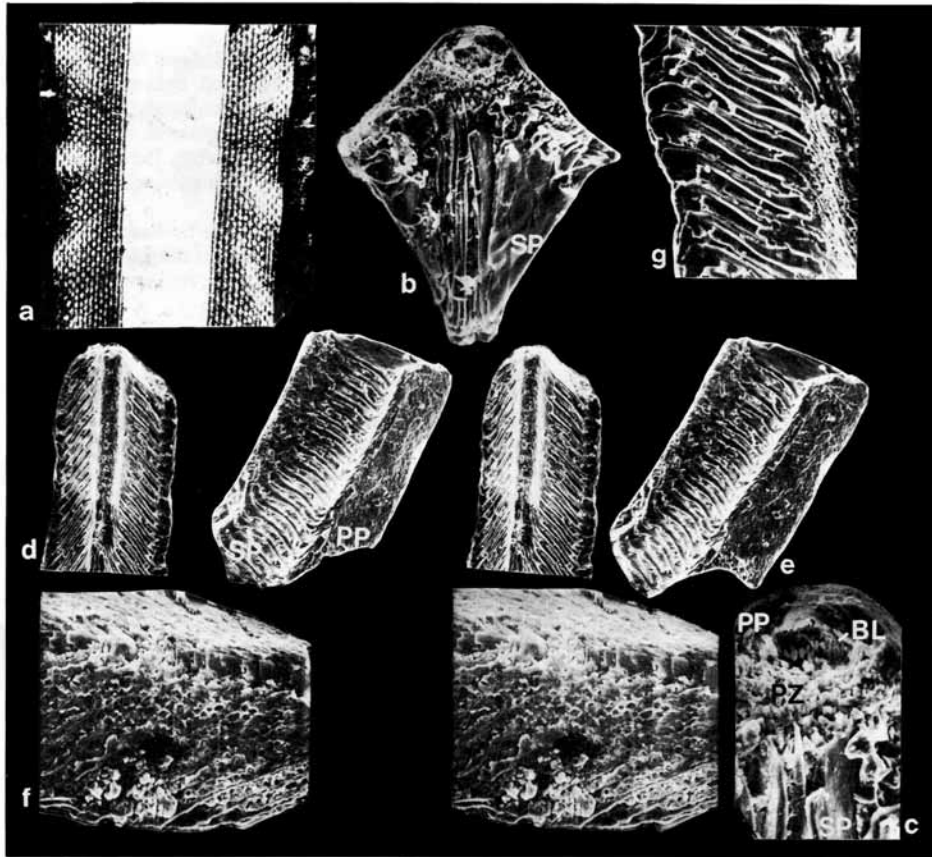
TEXT-FIG. 4. *a*, longitudinal section through the shaft of a primary spine of *Archaeocidaris urei* (Fleming) (HM E143). The hollow lumen is filled with clear calcite, ×20; *b–g*, tooth of *Eodiadema* aff. *minutum* (Buckman); *b*, cross-section, abaxial edge to the top, ×220. *c*, enlargement of same showing basal lamella of prism zone (BL), ×450. *d*, stereo view of the axial face, ×110. *e*, stereo view of the lateral face, ×110. *f*, stereo view of dorsal face: primary plates partially covered by a retiform layer of sterom, ×260. *g*, axial face showing secondary plates, ×260. Abbreviations, see text-fig. 2.

The demi-pyramids of *Eodiadema* are like those of juvenile *Diademopsis* but for the dense calcite buttress running from the processus superioris to the intrapyramidal suture. They also resemble the demi-pyramids of the irregular echinoids *Holectypus* and *Echinolampas* (see Kier, 1974, Märkel, 1978, and text-fig. 6J, K). In *Echinolampas* the foramen magnum is shallower, though still broad and U-shaped, and the lateral part of the abaxial face rather more developed.

Comparison with other lanterns

This lantern is like the lantern found in juvenile cassiduloids and in many respects is intermediate between the regular *Diademopsis*-type of lantern and the lanterns seen in irregular cassiduloid or holectypoid echinoids. Although no epiphyses, rotulae or compasses were found in the shale samples,

this does not mean that they were not present in *Eodiadema*, as they could easily have been overlooked.

Because the demi-pyramids are strongly curved, the lantern of *Eodiadema* was probably recumbent, as in *Echinolampas*. A recumbent posture, broad heart-shaped outline and broad foramen magnum are all features found in lanterns of juvenile cidarids and euechinoids (Lovén, 1892, Jackson, 1912). These features are also typical of the lanterns of many Palaeozoic echinoids. As *Eodiadema* is rarely larger than 1 cm in diameter and has rather advanced teeth, the shape of the pyramids is much more likely to be a juvenile feature retained by neoteny than an original primitive character.

Mortensen (1933) described the lantern of the Sinemurian (Lower Liassic) *Eodiadema collenoti* Cotteau. In this species the demi-pyramids are narrow, the foramen magnum is deep and unusually broad and the teeth are grooved. The differences between the lanterns of these two species suggests that the genus *Eodiadema* is more diverse than has previously been recognized.

EVOLUTION OF THE LANTERN IN POST-PALAEOZOIC ECHINOIDS

The studies of Märkel (1969–1979) and Jensen (1974, 1979, 1980) have added greatly to our knowledge of tooth and lantern structure of living echinoids, and both workers have used their findings for interpreting echinoid phylogeny, arriving at different conclusions. The evolution of this complex apparatus is difficult to interpret simply from the comparative morphology of living echinoids as all present day lanterns have advanced features not present in ancestral lantern.
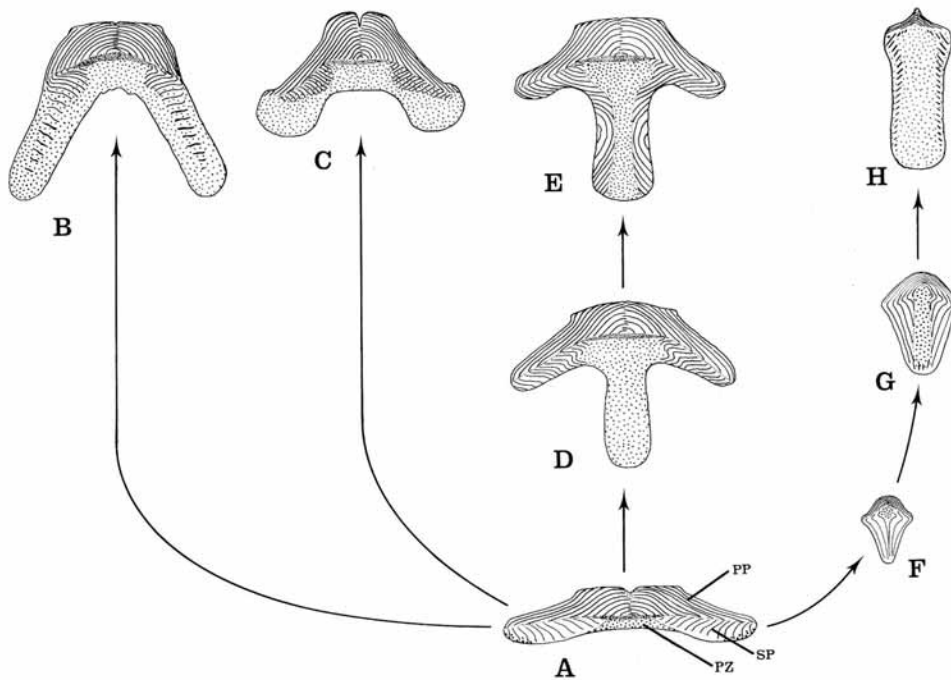
Teeth

Although the detailed structure of archaeocidarid teeth is as yet undescribed, it is probably very similar to that found in *Diademopsis*, as both are similar in shape. Cidarids, echinothurioids and diadematoids all appear to have inherited much the same tooth structure from their common ancestor. *Diademopsis* teeth are made up of primary echinothuriid-type plates with well-developed secondary plates lacking extensions and a relatively thin central zone of prisms. Two small areas of prisms also occur laterally.

In cidaroids such as *Stylocidaris*, the tooth has become more U-shaped in cross-section but has retained much the same structure with primary plates, secondary plates without extensions and an axial prism zone. However, the prism zone is considerably thicker in cidaroids particularly at the lateral edges. In the *Diademopsis*-type of tooth there was both a central-lamellae-needles-prisms (CLNP) complex and a lateral-lamellae-needles-prisms (LLNP) complex (the structures from which the prism zone develops—see Märkel and Titschack, 1969) but the LLNP complex must have been poorly developed. In cidaroids, the LLNP complex has expanded and developed to produce the broad prism zone.

Diadematoid teeth are similar to cidaroid teeth in their structure (though differing in the arrangement of their CLNP and LLNP complexes—Märkel, 1970a, Jensen, 1979) and are thicker and more U-shaped in cross-section than *Diademopsis*-type teeth (compare text-figs. 5A and 5C). The prism zone is thick and forms the entire axial face in *Centrostephanus* but in *Micropyga* the secondary plates are extensive and the prism zone small and central (Märkel, 1970a).

Both cidarids and diadematoids have evolved a thicker, more U-shaped tooth than was probably present in their latest common ancestor and in both groups the LLNP complex has developed and the prism zone expanded. These are adaptations for strengthening the tooth. The prism zone of longitudinal calcite rods is well suited to withstand tensional stress whereas the laminated zone of plates is best suited to withstand compressional stress (see Märkel and Gorny, 1973, Märkel, Gorny and Abraham, 1977). The prism zone has expanded and thickened adaxially and the tooth become more U-shaped in cross-section to produce a stronger tooth, better adapted for grazing and better able to withstand bending stresses. Apparently cidarids and diadematoids evolved this stronger type of tooth independently as a result of similar selection pressures. The U-shaped cross-section and the

TEXT-FIG. 5. Cross-sections of teeth showing the suggested evolutionary advances from the *Diademopsis*-type of tooth. A, *Diademopsis*. B, cidarid (*Stylocidaris*). C, diadematoid (*Centrostaphanus*). D, stirodont (*Stomopneustes*). E, camarodont (*Paracentrotus*). F *Fodiadema*. G, clypeasteroid (*Echinocyamus*). H, clypeasteroid (*Encope*). PP, primary plate: PZ, prism zone: SP, secondary plate. (B after Märkel and Titschack, 1969: C after Märkel, 1970a: D, E after Märkel, 1969: G after Märkel, 1978: H after Märkel, 1974.)

expanded LLNP complex and prism zone are both convergent features and this may explain why cidarids and diadematoids have somewhat different CLNP and LLNP complexes.

The structure of keeled stirodont teeth is not very different from the structure of the *Diademopsis*-type of tooth and Märkel (1970a) has already pointed out the similarity between echinothurioid teeth and keeled teeth. Keeled stirodont teeth differ from the *Diademopsis*-type of tooth only in the relative development of the prism zone and could have evolved from it by adaxial expansion of the central prism zone coupled with loss of the small lateral prism zones. Stirodonts have thus evolved a stronger type of tooth in a different way to cidarids and diadematoids. Although both have expanded their prism zone, this has occurred laterally in cidarids and diadematoids but axially in stirodonts. It is easy to see how the camarodont-type of keeled tooth could be derived from the stirodont-type of keeled tooth by the development of carinal appendages on the secondary plates.

The origin of the diamond- and wedge-shaped teeth of irregular echinoids has been under dispute. Märkel (1970b, 1974) emphatically rejected the view that the teeth of clypeasteroids could be derived from 'cidaroid ancestors or any of their descendants'. He later modified his views slightly with the discovery of similar teeth in cassiduloids (Märkel, 1978) maintaining that the teeth of regular and irregular echinoids are fundamentally different and that the diamond-shaped teeth of cassiduloids

came closer to the ancestral type of tooth than did any other type of tooth of living echinoids. Jensen (1979) rejected Märkel's ideas and argued for the derivation of diamond- and wedge-shaped teeth from echinoid teeth with simple secondary tooth plates lacking carinal appendages. She favoured derivation of irregular echinoids from an aulodont ancestor.

I agree with Jensen and can find no evidence in support of Märkel's views. The type of rhombic tooth found in *Eodiadema* and irregular echinoids could be derived from a *Diademopsis*-type of tooth by expansion of the secondary plates and a slight reduction in the prism zone. These changes may have been brought about through neoteny. *Eodiadema* is a minute echinoid and it has been shown above that the pyramids have typical juvenile characteristics. Echinoid teeth change shape as they grow and newly formed primary plates of grooved, keeled, and diamond-shaped teeth are triangular in shape and more or less indistinguishable (Märkel, 1978, Jensen, 1979). Lateral elongation takes place at a later stage in regular echinoid teeth as does the development of the LLNP complex. I suggest that, by arresting the growth of primary plates before they became strongly elongate and before the LLNP complex had developed, diamond-shaped teeth could be derived from grooved teeth simply by precocious formation of secondary plates. This would explain the loss of the LLNP complex and the restriction of the prism zone to a small central region in diamond-shaped teeth. This homologizes the lateral plates of diamond-shaped teeth with secondary plates of keeled and grooved teeth. Jensen (1979), however, has used the absence of an LLNP system to argue that lateral plates are extensions of primary plates. I believe that the diamond-shaped tooth evolved in *Eodiadema* or a close relative through fixation and modification of juvenile characteristics in a group that reached sexual maturity at an early growth stage. The more specialized wedge-shaped teeth of clypeasteroids are easily derived from the diamond-shaped teeth seen in *Eodiadema*, holectypoids, and juvenile cassiduloids. Text-fig. 5 summarizes the probable evolutionary development of tooth structure in post-Palaeozoic echinoids.

The lantern

The lantern of archaeocidarids is inclined and pyramids are broad and heart-shaped with a wide, moderately deep and U-shaped foramen magnum (Jackson, 1912: text-fig. 6A). All living regular echinoids, except for echinothurioids, have upright lanterns and consequently their pyramids are much narrower (the lantern circumference having been greatly reduced). This change occurred twice independently, once in the cidaroids and once in the euechinoids, and probably became feasible with the development of a more or less rigid test.

The perignathic girdle and lantern of cidarids are quite different from those of euechinoids, suggesting an independent derivation. In cidarids, the foramen magnum is more or less lost (text-fig. 6B), rotulae and epiphyses have evolved a ball and socket joint (see Märkel, 1979) and the lantern support structures are interambulacral apophyses. In euechinoids, the foramen magnum is a deep, V-shaped notch, rotulae and epiphyses have a hinge joint and the lantern support structures are ambulacral auricles. Neither type could be derived easily from the other but both could be derived from the archaeocidarid arrangement.

The lantern of echinothurioids has a number of primitive features. In phormosomids (text-fig. 6C), the lantern is strongly reclined, has a broad, U-shaped foramen magnum, no processi supra alveolaris and the epiphyses have more or less lost their demi-arc. In echinothuriids (text-fig. 6D) and pelanechinids, the lantern is rather more upright, has a slightly deeper and narrower foramen magnum, has axially projecting processi supra alveolaris and epiphyses with finger-like demi-arcs. Both groups have well-developed auricles.

The earliest known upright lantern of euechinoids is seen in *Diademopsis*. Pyramids have a deep, V-shaped foramen magnum but lack processi supra alveolaris. Epiphyses are flat with a prominent demi-arc. With the evolution of a deep foramen magnum much of the tooth was left unsupported, whereas in archaeocidarids and cidarids the tooth is supported along most of its length by the dental slide. Many euechinoid groups have extensions of the processus superioris (the processi supra alveolaris) that help support the growing end of the tooth by providing support for a membrane (text-fig. 6F, G). In echinothuriids and pelanechinids, the processi supra alveolaris extend axially whereas in

other groups they tend to arch more over the foramen magnum. With the development of these extensions, the epiphyses started to lose their broad demi-arcs which, in some cases, evolved into a narrow projection resting on top of the processus supra alveolaris. The tooth in camarodonts is supported by enlarged epiphyses that have become sutured together (text-fig. 6H). Presumably, with the development of firmly sutured epiphyses, the processi supra alveolaris were no longer required for support and were lost. The evolution of a deep foramen magnum probably occurred to make the lantern lighter and give it more mobility.

The pyramids of *Eodiadema* differ little from the pyramids of juvenile *Diademopsis* and are very like the pyramids in holectypoids and juvenile cassiduloids. The lantern of *Camerogalerus cylindrica* (Lamarck), illustrated by Hawkins (1909), is very similar to the lantern of *Eodiadema*. *Holectypus* (text-fig. 6J) has a large lantern with a very deep and broad foramen magnum that extends at least two-thirds of its height. It also has very broad epiphyses. Both of these features suggest that the lantern circumference was large and the pyramids inclined. The lantern of *Holectypus* differs from the
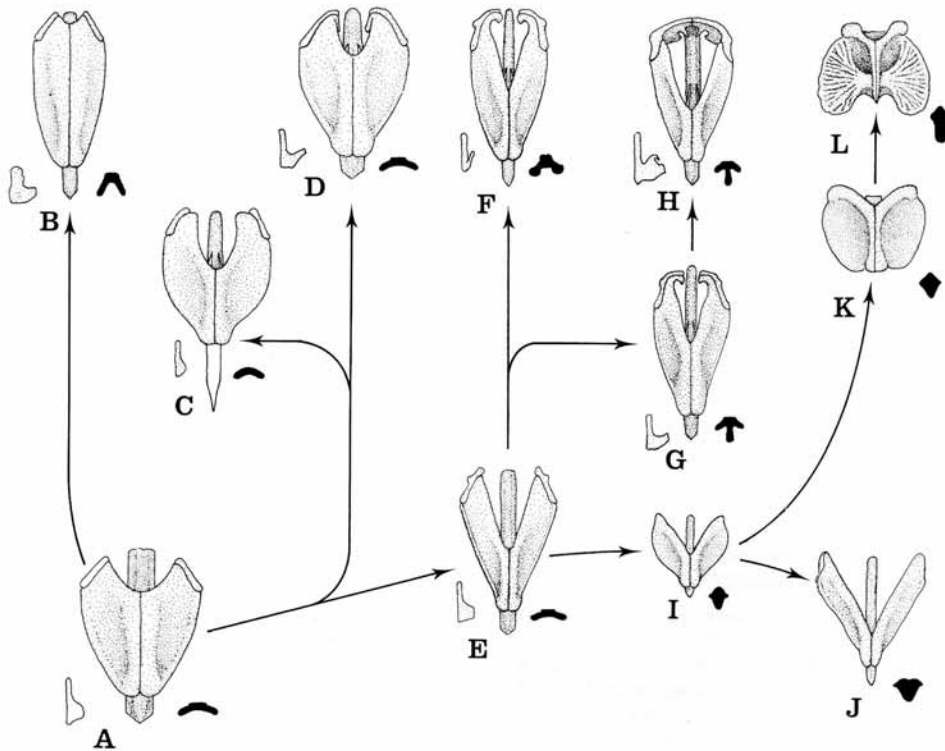
TEXT-FIG. 6. Diagram summarizing the suggested evolution of the pyramid (centre), epiphysis (left-hand side) and tooth cross-section (right-hand side). A. Archaeocidarid (*Archaeocidaris*). B. Cidarid (*Eucidaris*). C. Phormosomid (*Phormosoma*). D. Echinothuriid (*Calveriosoma*). E. Early 'pedinoid' (*Diademopsis*). F. Diadematoid (*Diadema*). G. Stirodont (*Arbacia*). H. Camarodont (*Strongylocentrotus*). I. *Eodiadema*. J. Holectypoid (*Holectypus*). K. Cassiduloid (*Echinolampas*). L. Clypeasteroid (*Echinocyamus*).

A–C, F–H modified from Jackson (1912); K, L after Kier (1974); J reconstructed from camera lucida drawings of BMNH E34472.

Eodiadema-type of lantern only in being at a more advanced stage of growth. The cassiduloid lantern is never functional and is present only in juveniles. This probably explains why it is so little modified from the *Eodiadema*-type of lantern.

In clypeasteroids (text-fig. 6L), the lantern is a functional crushing apparatus and has undergone profound modification. Although intermediate forms of pyramid have not yet been reported, it seems probable that the clypeasteroid type of lantern evolved from a cassiduloid-type of lantern. Text-fig. 6 summarizes the probable evolutionary development of the lantern in post-Palaeozoic echinoids.

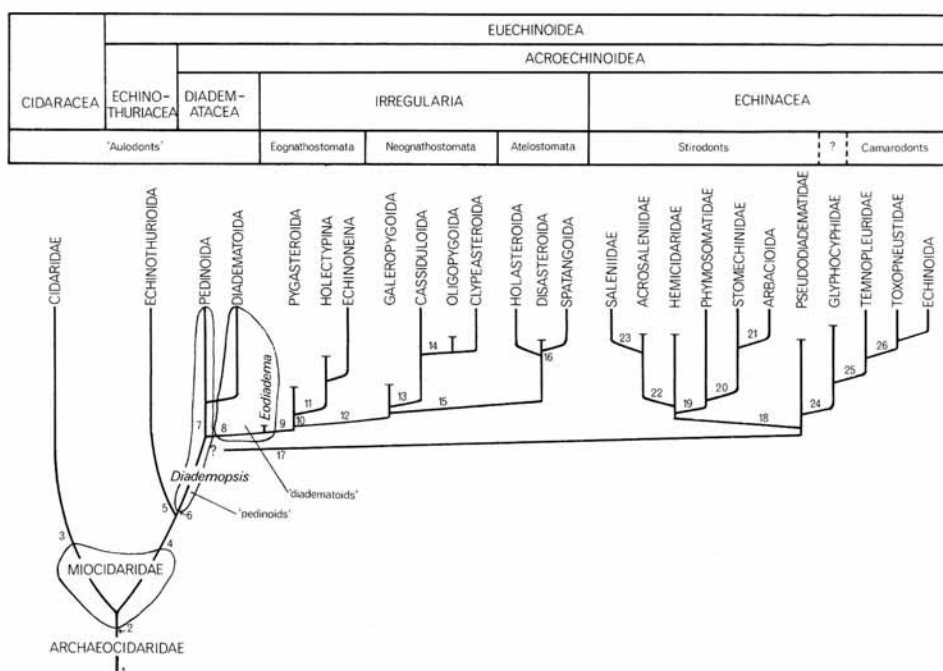## PHYLOGENY OF POST-PALAEOZOIC ECHINOIDS

In 1957 Durham and Melville published a phylogeny of the Echinoidea which derived all living echinoid groups from the miocidarids. This phylogeny gained widespread acceptance and was republished in a slightly modified form in the *Treatise on Invertebrate Paleontology* (Durham, 1966). Just before publication of the *Treatise*, Philip (1965) produced an alternative phylogeny in which all groups were derived from lepidocentrid ancestors with cidaroids, stirodonts and camarodonts more closely related to one another than to any other group. His views have not received much support from other workers. In recent years, there has been growing evidence to suggest that some of Durham and Melville's ideas were mistaken.

On the basis of his work on tooth structure in living echinoids, Märkel (1970–1979) has proposed a rather different phylogeny deriving clypeasteroids from an unknown Palaeozoic ancestor and regular echinoids from a cidaroid ancestor. Using cladistic methodology, Märkel produced a phylogeny of regular echinoids in which echinothurioids were placed as the most advanced aulodonts and primitive sister group of stirodonts and camarodonts. I have argued above that the similarity of echinothurioid teeth to keeled teeth is symplesiomorphic not synapomorphic and, taking other features into consideration, there is considerable evidence for placing echinothurioids as the most primitive of all euechinoids.

Lewis and Jefferies (1980) have also applied cladistic methodology in determining the phylogenetic relationships of the salenioids. They homologize the sur-anal plates of salenioids with small plates incorporated into the apical system of irregular echinoids. They treat this as a synapomorphy suggesting that irregular echinoids are more closely related to salenioids than to any other group of regular echinoid. However, this scheme almost totally ignores data on the structure of the spines and lantern apparatus and their hypothesis is unacceptable when these data are taken into account.

The phylogeny of post-Palaeozoic echinoids proposed here is based on the evolution of advanced characteristics, as proposed by Hennig (1966) and takes into account much new information not available to Durham and Melville. The phylogeny is summarized in text-fig. 7 and each evolutionary step is discussed separately below.

1. The archaeocidarids are ancestral to both cidarids and euechinoids, and are best considered as the most advanced part of the stem group from which all living echinoids evolved. A stem group comprises all extinct members leading to the latest common ancestor of the crown group (in this case, living echinoids) but excluding earlier forms that were ancestral to other extant groups (see text-fig. 9). The archaeocidarids are characterized by the following: test flexible, composed of imbricating plates; ambulacra narrow, simple (but with larger tubercles on every third plate), composed of two columns and extending on to the peristome; interambulacra broad, composed of two or more columns; each interambulacral plate with a single, large, perforate, non-crenulate tubercle; spines hollow and lacking a cortext (text-fig. 4a) (Kier, 1965, has however reported finding an archaeocidarid with solid spines); perignathic girdle undeveloped; lantern oblique; pyramids broad, heart-shaped; foramen magnum moderately deep, U-shaped; articulation between rotulae and epiphyses hinge-jointed; teeth broad, weakly grooved, crescentic in cross-section, externally resembling teeth of *Diademopsis* (internal structure unknown); plate structure labyrinthic.

CIDARACEA	EUECHINOIDEA				
	ACROECHINOIDEA				
	ECHINO-THURIACEA	DIADEM-ATACEA	IRREGULARIA		ECHINACEA
	'Aulodonts'		Eognathostomata / Neognathostomata / Atelostomata		Stirodonts / ? / Camarodonts

Cladogram labels (left to right): CIDARIDAE, ECHINOTHURIOIDA, PEDINOIDA, DIADEMATOIDA, PYGASTEROIDA, HOLECTYPINA, ECHINONEINA, GALEROPYGOIDA, CASSIDULOIDA, OLIGOPYGOIDA, CLYPEASTEROIDA, HOLASTEROIDA, DISASTEROIDA, SPATANGOIDA, SALENIIDAE, ACROSALENIIDAE, HEMICIDARIDAE, PHYMOSOMATIDAE, STOMECHINIDAE, ARBACIOIDA, PSEUDODIADEMATIDAE, GLYPHOCYPHIDAE, TEMNOPLEURIDAE, TOXOPNEUSTIDAE, ECHINOIDA

Other labels: *Eodiadema*, *Diademopsis*, 'diadematoids', 'pedinoids', MIOCIDARIDAE, ARCHAEOCIDARIDAE

TEXT-FIG. 7. The phylogeny of post-Palaeozoic echinoids. Steps 1–26 are discussed in the text.

2. The family Miocidaridae Durham and Melville evolved from the archaeocidarids by the reduction of interambulacra to two columns of plates. The morphological diversity of this family has recently been shown by Kier (1977) and it is undoubtedly paraphyletic, as noted by Durham and Melville (1957). By the late Permian, one group (including *Miocidaris*) had evolved solid spines with a cortex and lantern support structures that are interambulacral apophyses. A member of this group presumably gave rise to the cidarids. Other genera, such as *Lenticidaris*, had developed apophyses and a more upright lantern with a reduced foramen magnum but retained hollow, cortex-free spines. The genus *Triadocidaris* even shows some incipient plate compounding (Bather, 1909; Kier, 1977). The miocidarids, therefore, include stem cidarids, stem euechinoids and probably the most advanced stem echinoids.

The latest common ancestor of living euechinoids is likely to have been a miocidarid with (*a*) an archaeocidarid lantern but with dorsal pitting; (*b*) incipient plate compounding; (*c*) perforate, non-crenulate tubercles; (*d*) hollow spines lacking a cortex; (*e*) perignathic girdle absent or weakly developed.

3. The family Cidaridae Gray share the following advanced characteristics: (*a*) perignathic girdle developed as apophyses; (*b*) lantern upright with narrow pyramids and greatly reduced foramen magnum; (*c*) spines solid and possessing a cortex; (*d*) rigid test; (*e*) U-shaped grooved teeth of the cidarid type; (*f*) plates composed of rectilinear stereom. Some of these features are already present in certain miocidarids. The ball and socket joint between rotulae and epiphyses has so far been reported only in *Eucidaris* and it is not yet clear whether this feature is present in all living cidarids (in which case it probably evolved in the miocidarid ancestor) or is more restricted.

4. Primitive regular euechinoids share the following synapomorphies: (*a*) plate compounding in the diadematoid manner; (*b*) perignathic girdle composed of ambulacral processes; (*c*) pyramids with a relatively deep foramen magnum, usually V-shaped; (*d*) dorsal pits on demi-pyramids; (*e*) gills, usually with accompanying gill slits; (*f*) ophicephalous pedicellariae; (*g*) sphaeridia.

5. The Echinothurioida Claus are here considered to be the primitive sister group of all other euechinoids. This group has the euechinoid synapomorphies listed above but has retained a large number of plesiomorphic features in common with its archaeocidarid and miocidarid ancestors. These include: (*a*) an imbricate, flexible test; (*b*) ambulacra that extend on to the peristome; (*c*) Stewart's organs; (*d*) an oblique lantern with a U-shaped foramen magnum; (*e*) shallowly grooved teeth.

Well-developed Stewart's organs are found only in echinothurioids and cidaroids and must have been present in the latest common ancestor of these groups (vestige Stewart's organs are also known in the Recent pedinoid *Caenopedina* and in two species of diadematoid). The compound plating found in Recent echinothurioids is highly advanced and differs from the type of plate array seen in other regular echinoids. Although Jurassic echinothurioids have a diadematoid-type of plate compounding, living echinothurioids usually show a more advanced compounding, with the development of occluded plates. The latest common ancestor of the euechinoids presumably had some form of weak compounding in the diadematoid manner and the echinothurioids have undergone a long period of divergent evolution. Similarly, the flexibility of the echinothurioid test is more pronounced than in miocidarids and must represent a more advanced condition. Although echinothurioids are only known as far back as the Bajocian (Mortensen, 1934; Hess, 1973), they have a very poor fossil record and probably evolved at some time in the late Triassic (see below).

Jensen (1979) has suggested that living echinothurioids can be divided into two groups (the Echinothuriidae and the Phormosomidae) on the basis of the structure of their teeth and the observations on lantern structure given above support this. As yet, however, too little is known about this interesting group of echinoids to determine the relationships of the two groups.

6. Other euechinoid groups of regular echinoid share the following synapomorphies not found in echinothurioids: (*a*) upright lantern; (*b*) rigid (sometimes weakly imbricate) test; (*c*) ambulacra not extending on to the peristome and peristomial tube feet reduced to ten; (*d*) narrow pyramids with a deep, V-shaped foramen magnum; (*e*) globiferous pedicellariae usually present; (*f*) reduction of loss of Stewart's organs; (*g*) prominent gill slits.

Diademopsis is probably typical of the stem members of this group for which I propose the name Acroechinoidea (Greek *Akros* = highest). The Acroechinoidea include all euechinoids except for Echinothurioida. *Diademopsis* has retained the following plesiomorphic features: (*a*) broad, shallowly grooved teeth with echinothuriid primary plates; (*b*) hollow spines lacking a cortex or external thorns; (*c*) flat epiphyses with a broad demi-arc; (*d*) weak diadematoid compounding of ambulacra; (*e*) demi-pyramids without processi supra alveolaris.

7. *Diademopsis* differs from more advanced members of the Pedinoida Mortensen and Diadematoida Duncan in several respects. The pedinoids and diadematoids share the following synapomorphies that are not found in *Diademopsis* but which were probably present in their latest common ancestor: (*a*) U-shaped teeth with a well-developed prism zone (except in the family Micropygidae Mortensen—see Märkel, 1970*a*) and diadematoid-type primary tooth plates; (*b*) a secondary calcite filling to the axial groove near the ventral point; (*c*) demi-pyramids with a processus supra alveolaris; (*d*) epiphyses with elongate demi-arcs; (*e*) shaft of spine thorned.

The processus supra alveolaris developed on demi-pyramids of the living pedinoid *Caenopedina* that were illustrated by Mortensen (1940) are much less well developed than those of diadematoids. Either demi-pyramids with a processus supra alveolaris evolved twice independently (once in the echinothurioids and once in other euechinoids) as suggested here or else early pedinoids and diadematoids are convergent in all the features listed in points 6 and 7, as proposed by Philip (1965), in which case the processus supra alveolaris was independently evolved in the pedinoids.

In diadematoids the spines usually remain hollow, the apical system has mostly insert occulars, tubercles become crenulate and gill slits are usually deep. The pedinoids retain weak gill slits and non-

crenulate tubercles but develop solid primary spines and a dicyclic apical system. The extant genus *Micropyga* (Family Micropygidae Mortensen) has non-crenulate tubercles and teeth with a small, restricted prism zone. This family was probably an early offshoot from the stem Diadematacea, as Jensen (1979) has suggested.

8. *Eodiadema aff. minutum* (Buckman) differs from the contemporary pedinoids in having crenulate tubercles and a cassiduloid-like lantern apparatus. It has been argued above that this type of lantern could be derived from a *Diademopsis*-type of lantern. The latest common ancestor that *Eodiadema* shared with the Diadematacea must have had (*a*) plate compounding of the diadematoid type; (*b*) *Diademopsis* teeth; (*c*) hollow, thorned spines; (*d*) demi-pyramids without a prominent processus supra alveolaris. This suggests that *Eodiadema* probably evolved from a stem diadematacean (a primitive 'pedinoid' according to traditional classifications).

9. The structure of the teeth of *Eodiadema* shows that this genus lies close to the latest common ancestor of all irregular echinoids. Early, primitive irregular echinoids have the following features in common with *Eodiadema*: (*a*) weakly developed ambulacral compounding in the diadematoid manner; (*b*) inclined lantern with a broad foramen magnum and no processi supra alveolaris; (*c*) gills and gill slits (secondarily lost in later groups); (*d*) perignathic girdle of auricles; (*e*) teeth diamond-shape in cross-section; (*f*) spines lacking a cortext and hollow (except possibly in pygasteroids); (*g*) perforate, crenulate tubercles; (*h*) simple cylindrical tube-feet, suckered both orally and aborally.

The synapomorphies of irregular echinoids as a whole are: (*a*) development of bilateral symmetry with the tendency of the anus to break out of the apical system, genital 5 pore lost and a tetrabasal apical system formed; (*b*) the reduction in size of spines and tubercles and the increase in number of spines and tubercles per plate.

Primitive irregular echinoids usually show some degree of plate imbrication (see Jesionek-Szymanska, 1968) which is presumably a symplesiomorphic feature inherited from their regular ancestors.

10. The relationship of the Pygasteroida Durham and Melville and Holectypoida Duncan to other echinoid groups has been much disputed. Mortensen (1948), Durham and Melville (1957), and Durham (1966) thought that pygasteroids and holectypoids evolved from different groups of regular echinoid and that irregular echinoids are in fact polyphyletic. Philip (1965) argued for irregular echinoids being a monophyletic group, as did Jensen (1979, 1980).

Since Jesionek-Szymanska (1970) showed that early pygasteroids had crenulate tubercles, the distinction between pygasteroids and holectypoids has rested on spine and lantern structure. Pygasteroids and holectypoids both retain their lantern as adults. It has been argued above that the extremely broad foramen magnum and rotulae seen in a specimen of *Holectypus* (BMNH E34472) point to the lantern having been inclined rather than upright. In *Pygaster*, little can be made out about the shape of the pyramids from the pieces of lantern described by Melville (1961) but the foramen magnum is again reported to be 'fairly wide' and the rotula figured is unusually broad, like the rotulae of *Holectypus*.

The teeth of *Pygaster* and *Holectypus* are rather similar, as pointed out by Kier (1974). In figures given by Melville (1961, Plate 29, figs. 1 and 2) the tooth of *Pygaster* appears to be roughly trapezoidal in cross-section and quite comparable with teeth of *Eodiadema*. However, another tooth shows a lateral groove and Melville based his reconstruction on this. I have examined the lantern of *Holectypus* figured by Durham and Melville (1957) and Kier (1974) (BMNH E34472.) It is badly worn but its teeth are clearly not as illustrated by Durham and Melville (1957, fig. 1). Contrary to the illustration given by Kier (1974, fig. 54), the abaxial face is not concave but very gently convex with a median groove (where the two columns of primary plates presumably meet). The axial face of the tooth is broad and triangular and there appears to be a weak flange developed between axial and abaxial faces (text-fig. 6J). The teeth of the holectypoids *Camerogalerus cylindrica* (Lamarck) (BMNH E9075 and illustrated by Hawkins, 1911) and *Dixonia dixoni* (Forbes) (BMNH E95376) have also been re-examined. They are diamond-shaped in cross-section and in general form are indistinguishable from teeth of *Eodiadema* and cassiduloids. Although the teeth of *Pygaster* and *Holectypus* are more

triangular than diamond-shaped in cross-section, they are much more like teeth of other irregular echinoids than any keeled tooth of a regular echinoid. The teeth of the living holectypoid *Echinoneus* were described by Westergren (1911) and his illustration shows them to be similar to other irregular echinoid teeth. I agree with Jensen (1979, 1980) that the lantern and teeth of *Holectypus* and *Echinoneus* cannot be stirodont.

As far as the evidence goes, the teeth and lanterns of holectypoids and pygasteroids are similar, and quite comparable with those in other irregular echinoids. The remaining difference between pygasteroids and holectypoids rests on the structure of their spines. Spines are hollow in holectypoids but are reported to be solid in *Pygaster* (Melville, 1961). The resemblance of these two groups in most other features suggests that the pygasteroids and holectypoids are very closely related. The pygasteroids plus holectypoids retain more primitive features than any other group of irregular echinoids and are taken as the primitive sister group to all other extant irregular echinoids.

11. The Pygasteroida Durham and Melville display very few advanced features and are considered to be the most primitive of irregular echinoids. Interambulacral tubercles are of various sizes, regularly arranged and sparse. The periproct still lies within the apical system in early species although genital 5 is later lost (*Pileus* is not considered by the author to belong to this group, but probably belongs to the Echinoneina Clark). If the pygasteroids do indeed have solid spines then this is an advanced feature that distinguishes them from the Holectypoida.

The Holectypina Duncan and Echinoneina Clark both have their periproct well removed from the apical system, usually positioned on the ventral surface, and are thus considered more advanced than the pygasteroids. The Holectypina (Families Holectypidae Lambert, Anorthopygidae Wagner and Durham and Discoididae Lambert) retain their lantern, perignathic girdle, and gill slits throughout life and may evolve internal buttressing and interambulacral ridges for supporting the radial auricles. Tuberculation is denser and more uniform in size compared with pygasteroids but remains orderly. The Echinoneina Clark (Families Echinoneidae Agassiz and Desor, Conulidae Lambert and Galeritidae Gray) have the following synapomorphies not found in Holectypina: (*a*) loss of gill slits; (*b*) lantern and perignathic girdle present only in juveniles or ?lost; (*c*) dense irregularly arranged tuberculation (except in *Conulus*).

12. The Galeropygoida Mintz are primitive irregular echinoids sharing the following synapomorphies: (*a*) small, central peristome lacking gill slits; (*b*) lantern and perignathic girdle absent in adults (though probably present in juveniles); (*c*) tubercles very small, numerous, uniformly sized and arranged irregularly; (*d*) development of an anal sulcus; (*e*) development of unidirectional locomotion as shown by the bilaterally symmetrical tubercle arrangement; (*f*) development of weak oral phyllodes.

The earliest member, *Eogaleropygus*, retains a number of plesiomorphic features in common with pygasteroids (see Jesionek-Szymanska 1978) and probably evolved from this group. The fact that, in galeropygoids, the periproct still lies within the apical system, although genital 5 is reduced and imperforate, rules out any possibility of deriving galeropygoids from holectypoids. The Pygasteroida are therefore a paraphyletic group having given rise to both galeropygoids and holectypoids.

13. The Cassiduloida Claus resemble galeropygoids in most features but share the following synapomorphies: (*a*) development of petals and specialized respiratory tube feet; (*b*) development of bourrelets; (*c*) further removal of the periproct from the apical system (in primitive cassiduloids the apical system still surrounds the periproct).

The lantern is known in detail in only one living cassiduloid, *Echinolampas* (Kier 1974; Märkel 1978). It is asymmetric, with various sized pyramids, has no compasses and has very much reduced rotulae and epiphyses. As these features are also found in the lanterns of oligopygoids and clypeasteroids, this type of lantern was presumably present in the latest common ancestor of the three groups and may even have been inherited from the galeropygoids. One group of cassiduloids, the Conoclypidae Zittel, retain their lantern as adults but its structure is not known in detail. Whereas Jurassic and Cretaceous cassiduloids have a tetrabasal apical system, all post Cretaceous cassiduloids (except for *Apatopygus*) have a monobasal apical system.

14. The Oligopygoida Kier and the Clypeasteroida Agassiz share the following synapomorphies: (*a*) demi-pyramids with broad lateral wings expanded ventrally and buttressed by lamellae; (*b*) monobasal apical system; (*c*) presence of pseudo-compound plating; (*d*) absence of phyllodes.

Clypeasteroids differ from oligopygoids in having: (*a*) accessory tube feet and a correspondingly modified water vascular system; (*b*) no demi-plates beyond the petals; (*c*) ambulacra broader than interambulacra on oral surface.

The clypeasteroids evolved from a stem cassiduloid, as first suggested by Kier (1970). The perignathic girdle of oligopygoids and cassiduloids is more or less identical and involves inter-ambulacral processes as well as ambulacral processes (Kier 1974). Clypeasteroids have either ambulacral processes (Clypeasterina *sensu* Kier 1970) or interambulacral processes (Scutellina *sensu* Kier 1970). As the lanterns of clypeasteroids and oligopygoids are so similar and the more advanced perignathic girdle and water vascular system are present in clypeasteroids, oligopygoids should therefore be placed as the primitive sister group to clypeasteroids.

15. The Disasteroida Mintz share the following plesiomorphic characteristics with galeropygoids: (*a*) gills, gill slits, lantern, and perignathic girdle all absent, at least in adults; (*b*) periproct in early forms enclosed by apical system but genital 5 imperforate; (*c*) all ambulacra identical, non petalloid, lacking specialized tube feet; (*d*) phyllodes weakly developed; (*e*) tubercles small, uniformly sized, dense and irregularly arranged.

They have evolved the following synapomorphies: (*a*) elongate and disjunct apical system; (*b*) weakly developed protosternous plastron; (*c*) peristome shifted towards the anterior.

The disasteroids clearly evolved from an early galeropygoid, as proposed by Mintz (1968). The Galeropygoida must therefore be an improper stem group to the Neognathostomata plus Atelostomata having apparently given rise to both cassiduloids and disasteroids.

16. The Holasteroida Durham and Melville (*sensu* Mintz, 1968) and the Spatangoida Claus share the following synapomorphies not present in the disasteroids: (*a*) non-disjunct tetrabasal apical system; (*b*) fascioles usually present; (*c*) ambulacrum III usually differentiated aborally from other ambulacra; (*d*) phyllodes well developed, probably with highly specialized penicillate tube feet (see Smith, 1980*a*); (*e*) specialized and complexly branched respiratory tube feet (may be secondarily lost); (*f*) well-developed plastron; (*g*) spines and tubercles functionally differentiated.

These features must have been present in the latest common ancestor of the two groups, which was undoubtedly a disasteroid. The disasteroids form part of the stem group to the monophyletic crown group of holasteroids plus spatangoids. Holasteroids have an elongate apical system, like disasteroids but have a meridosternous plastron. Spatangoids are probably slightly more advanced as they have a compact tetrabasal apical system and an amphisternous plastron.

17. The stirodont and camarodont orders of regular echinoids form a well-defined, monophyletic group, but their phylogeny is difficult to disentangle. All possess keeled teeth and solid spines, both of which are synapomorphies. It was argued above that the keeled tooth probably evolved from a *Diademopsis* type of tooth. Although keeled teeth have not yet been reported from rocks older than the Middle Jurassic (Kier, 1974), members of stirodont orders are found as far back as the Upper Triassic (Kier, 1977). The structure of keeled teeth is fairly uniform (see Märkel 1969) and must have been inherited from the latest common ancestor of this group. Camarodont keeled teeth differ only in having a better developed carinal appendage on secondary tooth plates and must have evolved from a stirodont keeled tooth. The latest common ancestor of the Echinacea must have possessed: (*a*) rigid test; (*b*) upright lantern with a deep, V-shaped foramen magnum, styloid processes and processi supra alveolaris; (*c*) keeled teeth; (*d*) ambulacra not extending on to peristome; (*e*) weak diadematoid plate compounding; (*f*) perignathic girdle of auricles; (*g*) perforate, crenulate tubercles; (*h*) solid spines with a central meshwork of stereom; (*i*) dicyclic apical system.

Most features listed suggest that the echinaceans evolved from a stem acroechinoid that had developed processi supra alveolaris on its demi-pyramids. The stem echinaceans would then have had

to evolve solid spines, crenulate tubercles and an axially expanded prism zone on the teeth, none of which pose any great problems.

18. The stirodont group that appears to retain most plesiomorphic characteristics is the Hemicidaroida Beurlen. This group is divided into two families, the Hemicidaridae Wright and the Pseudodiadematidae Pomel. Hemicidarids have dense spines with a cortex and their ambulacra narrow markedly above the ambitus. Oral ambulacral plates are compound in the diadematoid manner though aborally they are usually simple. Pseudodiadematids have rather broader ambulacra that are compound throughout and spines with a mesh-filled core but without a cortex.

Unlike most previous workers, I believe that the pseudodiadematids are the more primitive group from which hemicidarids and other stirodonts arose. *Pseudodiadema* is in fact the oldest known echinacean (Kier, 1977) and some early pseudodiadematids are reported to have hollow spines (Melville, 1961). It is most likely that some of the early pseudodiadematids will prove to be stem echinaceans. The hemicidarids have come to resemble cidarids. Both have narrow sinuous ambulacra, a single large primary tubercle to each interambulacral plate and solid, massive spines with a well-developed cortex. However, the structure of the hemicidarid lantern and other euechinoid synapomorphies show that it could not possibly have evolved from cidaroid ancestors directly. The external resemblance between cidarids and hemicidarids must be due to convergent evolution and these features in hemicidarids are therfore synapomorphic with respect to the pseudodiadematids. Hemicidarids and cidarids presumably evolved to fill the same general niche and were subjected to the same sorts of selection pressures.

19. The Phymosomatidae Pomel show many of the plesiomorphic features of the echinaceans but have evolved imperforate tubercles. Early members of this group (i.e. *Jacquiertia, Leptechinus*) resemble hemicidarids in their narrow, often simple ambulacra, and like them have spines with a collar and thin cortex. They are therefore placed as an early offshoot of the hemicidarids that developed imperforate tubercles. Later members of the Phymosomatidae evolved polyporous plates with phymosomatid-type plate compounding.

20. The Stomechinidae Pomel differ from the phymosomatids in having non-crenulate tubercles and spines that lack a distinct cortex. The loss of the cortex is considered here to be a secondary feature. Stomechinids still possess massive spines and the arbacioids (which are here derived from the Stomechinidae) still retain the ability to form a thin cortex.

21. The Arbacioida Gregory were considered to have evolved from the Plesiocidaroida Duncan by Durham (1966) because of the resemblance of the latter to juvenile arbacioids. However, both Bather (1909) and Kier (1977) preferred to place plesiocidaroids as aberrant cidaroids. Until the lantern is discovered, plesiocidaroids will probably remain problematic, but they certainly have too many peculiar features to have been ancestral to the arbacioids. The tooth and lantern structure clearly show that arbacioids evolved from stirodont ancestors. Like stomechinids, arbacioids possess imperforate, non-crenulate tubercles and some stomechinids (e.g. *Psephechinus, Polycyphus*) have arbacioid-type plate compounding and markedly enlarged oral tubercles, both features typical of arbacioids. The plate construction of stomechinids and arbacioids is also very similar (Smith 1980b). Arbacioids therefore probably evolved from the Stomechinidae. Arbacioids have evolved the following synapomorphies not present in stomechinids: (a) arbacioid-type primary tooth plates; (b) anal valve in the periproct; (c) specialized aboral respiratory tube feet.

22. The Acrosaleniidae Gregory are very similar to the hemicidarids, differing principally in having one or more sur-anal plates incorporated into the apical system. This is taken as a synapomorphy.

23. The Saleniidae Agassiz, like acrosaleniids, have sur-anal plates incorporated into the apical system but have the advanced characteristic of having imperforate tubercles. Some saleniids have undergone secondary simplification returning to ambulacra composed entirely of simple plates.

24. Primitive Glyptocyphidae Duncan, such as *Glyptodiadema*, are similar to pseudodiadematids in having: (a) solid, ribbed spines lacking a cortex; (b) perforate, crenulate tubercles; (c) relatively

broad ambulacra compound in the diadematoid manner. The principal features that distinguish glyptocyphids from pseudodiadematids are their surface ornamentation and pitting (which is not well developed in early forms) and their apical system, which usually includes some insert occulars. Both features are synopomorphies. Mortensen (1943) and Durham and Melville (1957) both thought that glyptocyphids probably possessed a camarodont lantern because of their resemblance to temnopleurids. Just when the camarodont lantern evolved cannot, however, be determined and there is no sound evidence on which to judge whether glyptocyphids are camarodonts or stirodonts.

25. The Temnopleuridae Agassiz, Toxopneustidae Troschel and Echinoida Claus all share the following synapomorphies: (*a*) camarodont lantern without processi supra alveolaris but with enlarged and sutured epiphyses; (*b*) keeled tooth with well-developed carinal appendage on secondary tooth plates; (*c*) ambulacra compounded in the echinoid manner; (*d*) imperforate tubercles.
  The earliest group, the temnoleurids, have crenulate tubercles and pronounced plate sculpturing, features which are also present in glyptocyphids. Some Cretaceous glyptocyphids, such as *Echinopsis*, even show a primitive form of echinoid-type plate compounding. Temnopleurids probably evolved from the glyptocyphids.

26. Toxopneustidae Troschel and Echinoida Claus have both lost the tubercle crenulation and surface sculpturing found in temnopleurids. Toxopneustids differ from the Echinoida principally in having deep gill slits. The Orthopsida Mortensen are a problematic group that possess: (*a*) camarodont lantern; (*b*) perforate, non-crenulate tubercles; (*c*) ambulacra that are simple or weakly compound in the diadematoid manner. Until this group is better known and particularly until a more detailed study of its tooth and lantern structure has been carried out, the Orthopsida are best left out of this scheme.

Summary

All living echinoids form a monophyletic group whose stem group includes archaeocidarids and some miocidarids as its most advanced members. Cidarids are the primitive sister group to the Euechinoidea and, within the Euechinoidea, echinothurioids are the primitive sister group to all other euechinoids. The name Acroechinoidea is proposed for the monophyletic group composed of all euechinoids exclusive of Echinothurioida. *Diademopsis* is placed in the stem acroechinoids. The Acroechinoidea comprises three major monophyletic groups, the Irregularia, the Echinacea and a third group consisting of pedinoids plus diadematoids. The stem group of the Irregularia includes *Eodiadema* as one of its most advanced members. There are three principal groups within the irregulars for which I propose the names Eognathostomata, Neognathostomata and Atelostomata. The Eognathostomata comprises holectypoids plus pygasteroids and is the primitive sister group to other irregular echinoids. The Neognathostomata, together with the Atelostomata, also form a monophyletic group, with *Eogaleropygus* as a probable member of the stem group evolved from a primitive pygasteroid. The Neognathostomata is monophyletic and consists of cassiduloids, oligopygoids, clypeasteroids, and some galeropygoids. Holasteroids and spatangoids form another monophyletic group, the Atelostomata, with disasteroids and some galeropygoids forming their stem group. The position of recognized orders of irregular echinoids in the phylogenetic scheme is summarized in text-figure 8. The Echinacea consists of two monophyletic groups with early, primitive pseudodiadematids as part of their stem group. The two groups comprise (i) Hemicidaridae, Acrosaleniidae, Saleniidae, Phymosomatidae, Stomechinidae, and Arbacioida, and (ii) Pseudodiadematidae, Glyptocyphidae, Temnopleuridae, Toxopneustidae, and Echinoida. A simplified phylogenetic tree, showing only the superorders, is given in text-figure 9.
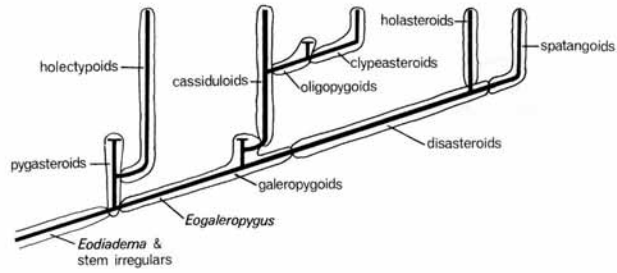
TEXT-FIG. 8. Phylogenetic tree of the Irregularia showing the probable
position of currently recognized orders.

COMPARISON WITH THE FOSSIL RECORD

The phylogeny shown in text-figure 7 is based entirely on morphological data. Apart from the initial assumption that archaeocidarids show plesiotypic features and were ancestral to all later echinoids, no account is taken of the fossil record. If the proposed phylogeny is valid then it should closely match the known history of post-Palaeozoic echinoids. Primitive sister groups should all make their appearance before their respective crown groups. In order to test this, the known stratigraphical ranges of post-Palaeozoic echinoids have been plotted (text-fig. 10) for comparison with text-figure 7. In nearly all cases primitive sister groups *do* appear earlier than crown groups and the phylogeny proposed here is quite compatable with the fossil record. There are, however, two discrepancies.

First, the Echinothurioida are a group with many morphological features that place them as the most primitive euechinoid group, yet they have not been found in beds older than the Middle Jurassic. This is rather puzzling until you consider whether there might be any reason for this gap in the fossil record. Echinothurioids are extremely poorly represented at any period in the past although today they are quite a diverse group. This is undoubtedly because they have a relatively meagre
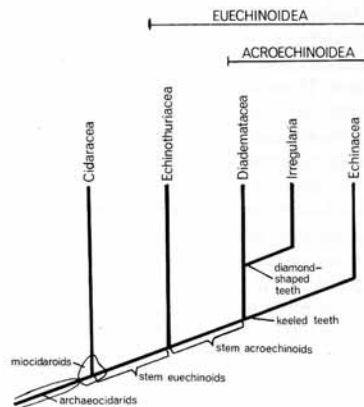
TEXT-FIG. 9. Simplified phylogenetic tree of
post-Palaeozoic echinoids showing only
superorders.
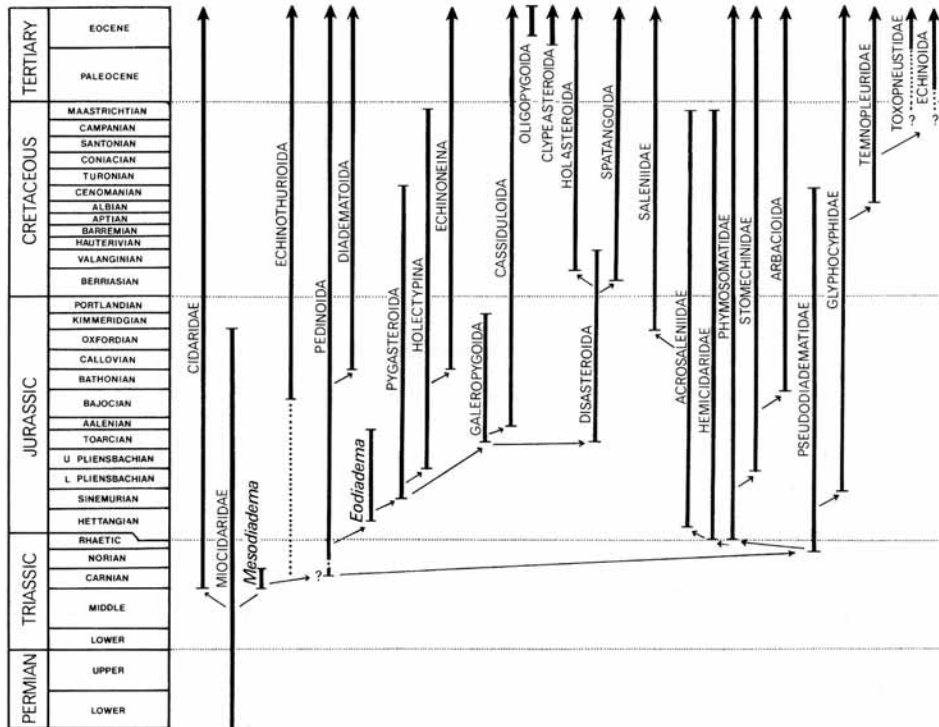
TEXT-FIG. 10. Stratigraphic range of currently recognized post-Palaeozoic echinoid groups (compare with text-fig. 7).

fossilization potential. Their test is thin, very fragile and readily dissociates upon death. More important, they now inhabit the deep ocean floor and have rarely been recorded in the shallower waters of the continental shelf where they stand some chance of being rapidly buried and preserved. If echinothurioids have always lived principally in this environment, as seems likely, then it is not really surprising that there are large gaps in their fossil record.

The second discrepancy is smaller and less important. Although both galeropygoids and disasteroids first appear in the Toarcian, disasteroids very slightly pre-date the earliest galeropygoids. This minor inconsistency is best explained by invoking the incompleteness of the fossil record.

Thirdly, there is some uncertainty as to when the Clypeasteroida first appear. Although this group is reported to range from the Upper Cretaceous onwards (Durham, 1966), Kier (1974, text-fig. 77) has been unable to confirm their presence in pre-Eocene rocks and doubted whether these reports were correct. The oligopygoids are restricted to the Middle and Upper Eocene, so that, according to the interpretation presented here, true clypeasteroids would not be expected in earlier beds. Whether or not this is true needs to be investigated.

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