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THE EVOLUTION OF *INOCERAMUS* IN
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[Quart. Journ. Geol. Soc., vol. lxxviii, 1912,
pp. 1-19.]

THE EVOLUTION OF *INOCERAMUS* IN THE CRETACEOUS PERIOD
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INTRODUCTORY REMARKS.

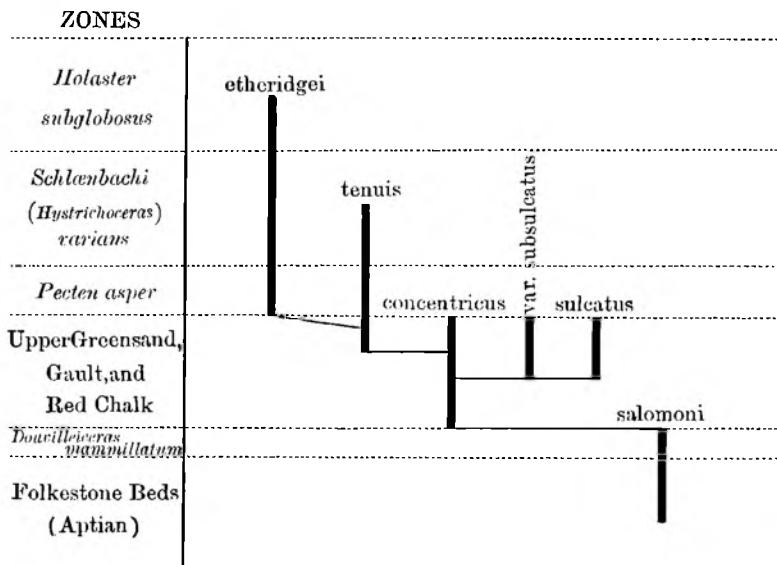
ALTHOUGH the genus *Inoceramus* is found in deposits as early as the Lias, yet it is represented by comparatively few species until the close of the Lower Cretaceous Period, after which it underwent rapid evolution so that many species and varieties were developed; but, so far as we know, none of these survived the Cretaceous Period or left descendants. From the evidence which has been furnished by a study of the variation of the species, their zonal distribution, morphological resemblances and development, and from the discovery of connecting links, it now seems possible to recognize the main lines of evolution in the *Inocerami* of the Cretaceous Period.

The species of *Inoceramus* found in the Gault, the Upper Greensand, and the Chalk appear to have originated from two stocks which occur in the Lower Greensand (Aptian), one being *I. salomoni* d'Orb., the other belonging to the type of *I. neocomiensis* d'Orb. and *I. ewaldi* Schlüt.

I. SPECIES CONNECTED WITH *INOCERAMUS SALOMONI*.

We may first deal with the species which are connected with *I. salomoni*, namely:—*I. concentricus*, *I. concentricus* var. *subsulcatus*, *I. sulcatus*, *I. tenuis*, and *I. etheridgei*, of which the distribution and relationship are shown in the accompanying diagram (A).

Diagram A.—*Distribution and relationship of the species connected with Inoceramus salomoni.*

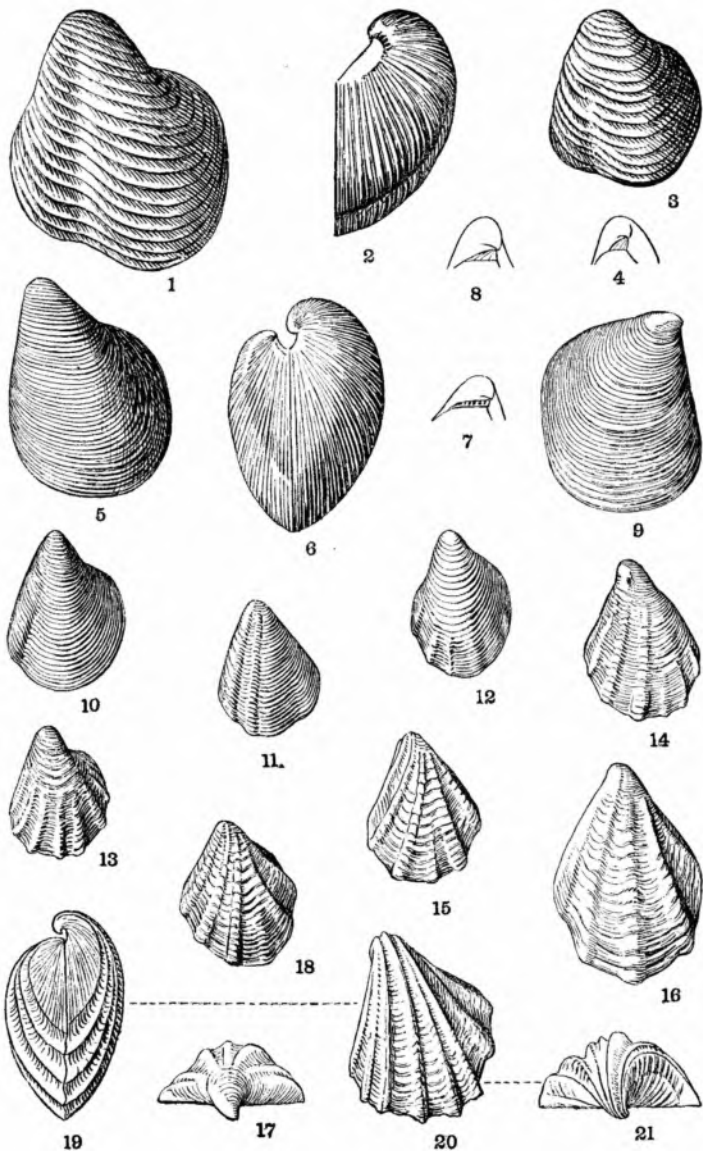


[The thick lines express the range of the species; the thin lines connecting them indicate what is believed to be the phylogeny of the species.]

I. salomoni d'Orb. (figs. 1–4, p. 3) is found in the Folkestone Beds (Lower Greensand) and in the *Mammillatum* Bed at the base of the Gault. The left valve is characterized by its subquadrate outline, the obliquely triangular hinge-area, the large anterior area bounded by a rounded ridge, the shallow radial sulcus which extends from below the umbo to the ventral margin and gives a sinuosity to the concentric ridges. In the early stage of growth the sulcus is not present, and the period at which it appears varies in different individuals.

I. concentricus Park. (figs. 5–9, p. 3)¹ ranges throughout the Gault and the Upper Greensand (with the exception of the zone

¹ For other figures, see H. Woods, 'Monogr. Cret. Lamellibr.' (Palaeont. Soc.), vol. ii (1911) pl. xlv, fig. 11, pl. xlvi, figs. 1–10, & pl. xlvi, figs. 1–2.



Figs. 1-4. *Inoceramus salomoni* d'Orb., *Mammillatum* Bed; left valves: 2, anterior view; 4, umbo and hinge-area. 5-9. *I. concentricus* Park., Gault: 5, left valve; 6, anterior; 7 & 8, umbo and hinge-area; 9, right valve. 10-18. *I. concentricus* var. *subsulcatus* Wiltsh., Gault: left valves. 19-21. *I. sulcatus* Park., Gault: 19, anterior; 20 & 21, left valve. All @ two-thirds of the natural size.

of *Pecten asper*), and is clearly of the same type as *I. salomoni*. In comparing it with *I. salomoni* we find that the early stage is similar, but of shorter duration; and after that stage is passed the left valve becomes more generally inflated, its axis of growth more oblique, the umbo narrower and more pointed, the anterior area smaller, the hinge-line shorter, and the hinge-area reduced in height. The radial sulcus is not developed. *I. concentricus* appears to have been derived from *I. salomoni* by the shortening of the hinge-line and the reduction in height of the hinge-area. Some forms of *I. concentricus* which possess a higher hinge-area (fig. 8, p. 3) and a rather larger anterior area than usual connect *I. concentricus* with *I. salomoni*.

I. sulcatus Park. (figs. 19–21, p. 3)¹ occurs in the Upper Gault, the Red Chalk, and the Upper Greensand (except in the zone of *Pecten asper*), and agrees closely with *I. concentricus*, notwithstanding the presence of strong radial folds which, at first sight, give it a very distinct appearance. Between these two species numerous intermediate forms (known as *I. concentricus* var. *sub-sulcatus* Wiltsh.) are found, in which every stage may be seen in the development of the radial folds (figs. 10–18, p. 3). The early part of the shell is identical with the adult shell of *I. concentricus*; in some cases this *concentricus* stage lasts for a considerable period (figs. 12 & 13); while in others it is of short duration (figs. 15–18), and in *I. sulcatus* (figs. 20 & 21) it is completely lost. The adult in some examples differs from *I. concentricus* only in the possession of a single radial fold (fig. 10); while in others two, three, or more (figs. 11–18) develop, until we get a type like *I. sulcatus*, in which the folds are sharp and numerous, and start from the apex of the umbo (figs. 20 & 21). On account of its strong radial folds, *I. sulcatus* has been placed by some authors in a separate genus or subgenus—*Actinoceramus*, Meek; but, since it has descended directly from *Inoceramus concentricus*, there is no reason for assigning it to a separate genus or subgenus.

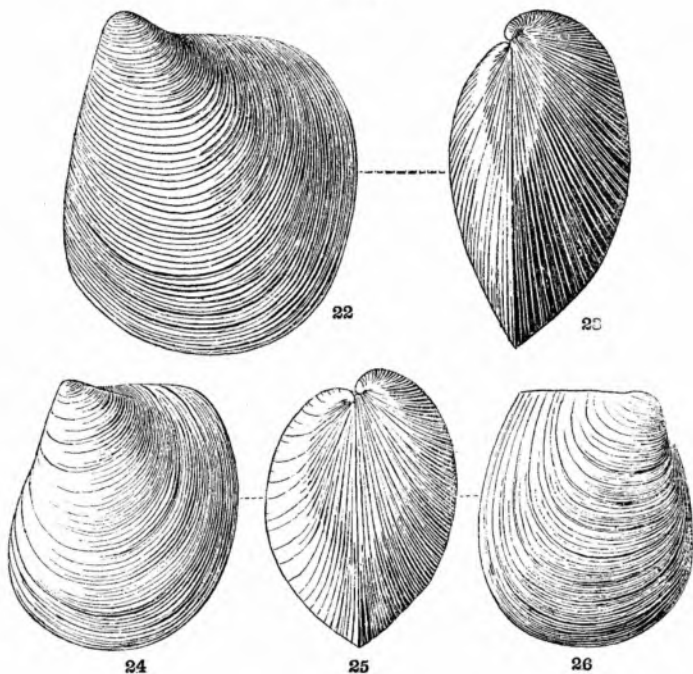
I. tenuis Mant. (figs. 22 & 23, p. 5)² ranges from the Red Chalk (= Gault) to the Chalk Marl (*varians* zone), and possesses most of the features of *I. concentricus*, from which it has clearly been derived; the main differences are its longer hinge-line and the less prominent umbo of the left valve.

I. etheridgei Woods (figs. 24–26, p. 5)³ extends from the zone of *Pecten asper* to the zone of *Holaster subglobosus*, and appears to have descended from *I. tenuis*. It possesses a similar concave anterior area and long hinge. The chief differences are found in the left valve, in which the umbo is less prominent, the postero-dorsal region is less compressed, and the valves are more nearly equal.

¹ H. Woods, *op. cit.* pl. xlvii, figs. 15–20.

² *Id. ibid.* pl. xlvi, fig. 1, & text-figs. 31–32.

³ *Id. ibid.* pl. xlix, figs. 2–4.



Figs. 22 & 23. *I. tenuis* Mant., Red Chalk : 22, left valve ; 23, anterior. 24-26. *I. etheridgei* Woods, *Holaster-subglobosus* Zone : 24, left valve ; 25, anterior ; 26, right valve. All @ two-thirds of the natural size.

II. SPECIES CONNECTED WITH *INOCERAMUS NEOCOMIENSIS*

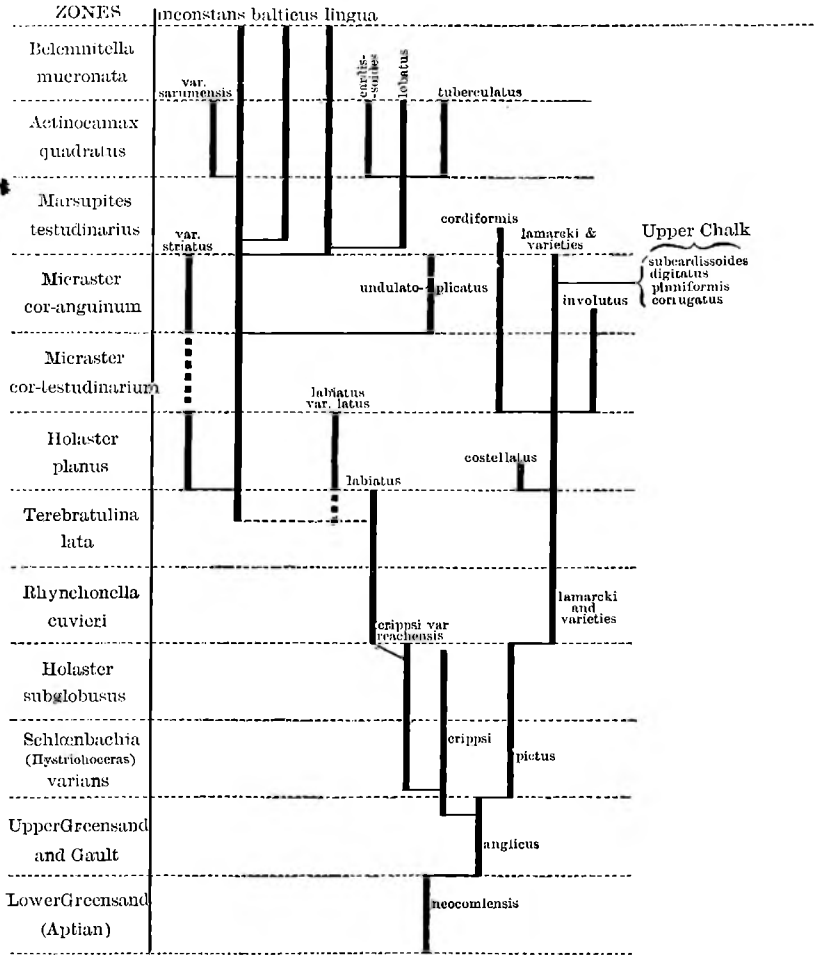
We may now consider the species which are believed to be connected with *I. neocomiensis*, the distribution and relationship of which are shown in the accompanying diagram (B, p. 6).

I. neocomiensis d'Orb. (fig. 27, p. 8) is found in the Lower Greensand, and a similar form (*I. ewaldi* Schlüt.) occurs in the Aptian of North Germany.

I. anglicus Woods (figs. 28, 29, 56, & 57)¹ occurs in the Gault, the Red Chalk, and the Upper Greensand, and appears to have arisen from a form of the type of *I. neocomiensis*. They agree in the general shape of the shell and in the type of ornamentation ; but in *I. anglicus* the posterior part of the shell is more compressed, while the part ventral to the umbones is more convex than in *I. neocomiensis* ; also in the former the ventral curvature of the ribs is sharper than in the latter. From *I. anglicus* two species seem to have arisen—*I. pictus* and *I. crippei*.

¹ H. Woods, *op. cit.* pl. xiv, figs. 8-10, & text-fig. 29.

Diagram B.—*Distribution and relationship of the species connected with Inoceramus neocomiensis.*



[The thick lines express the range of the species; the thin lines connecting them indicate what is believed to be the phylogeny of the species.]

I. pictus Sow. (figs. 30 & 31, p. 8)¹ ranges from the Chalk Marl (*varians* zone) to the zone of *Holaster subglobosus*; it resembles the forms of *I. anglicus* which have more numerous and more regular ribs (figs. 28 & 29). In *I. pictus* the ribs have become smaller, more numerous, and more regular; the anterior area is better developed, and is concave or nearly flat; and the shell is relatively shorter and higher than in *I. anglicus*.

I. lamarcki Park. (figs. 32-41, p. 8) begins in the zone of *Rhynchonella cuvieri* and extends to that of *Micraster cor-anguinum*. Some early forms of this species (*I. lamarcki* var. *apicalis* Woods, figs. 32 & 33),² in which the valves are only slightly unequal, the concentric folds not much developed, and the posterior ear not sharply limited, closely resemble *I. pictus*, and seem almost certainly to have descended from that species.³ *I. lamarcki* shows a great amount of variation,⁴ so that many of the forms have diverged considerably from *I. pictus* owing to change in convexity, in the number, strength, and curvature of the concentric folds, in the size and distinctness of the posterior ear, and in the relative height of the shell, etc.

In *I. lamarcki* var. *cuvieri* Sow. (figs. 40 & 41),⁵ which ranges from the zone of *Terebratulina lata* to that of *Micraster cor-anguinum*, the shell is high, with the valves only slightly convex and not very unequal, and with the concentric folds often absent or indistinct though sometimes becoming more or less strongly developed.

In forms like the type of *I. lamarcki* Park. (figs. 34-36) the valves are inflated and usually very unequal, the umbones prominent, the posterior ear sharply defined, and the concentric folds well-developed. Other similar forms have the posterior ear indistinctly limited, and the folds may be only poorly developed. The left valve is sometimes very much more convex than the right (fig. 38), and occasionally the two valves are of nearly equal convexity (fig. 37).

I. lamarcki var. *websteri* Mant. (fig. 39) occurs mainly in the zone of *Micraster cor-testudinarium*; it is an inflated form with the posterior ear not sharply limited, and is distinguished by the very thin shell and the sharp ridge-like character of the concentric folds.

I. involutus Sow. (figs. 44-47, pp. 9 & 10), found in the zone of *Micraster cor-testudinarium* and in the lower part of the zone of *M. cor-anguinum*, is shown by intermediate varieties (figs. 42 & 43, p. 9) to have descended from a convex form of *I. lamarcki*, by the increase in size and convexity of the left valve, its acquirement of a spirally curved umbo, the loss of concentric folds, and the loss of the

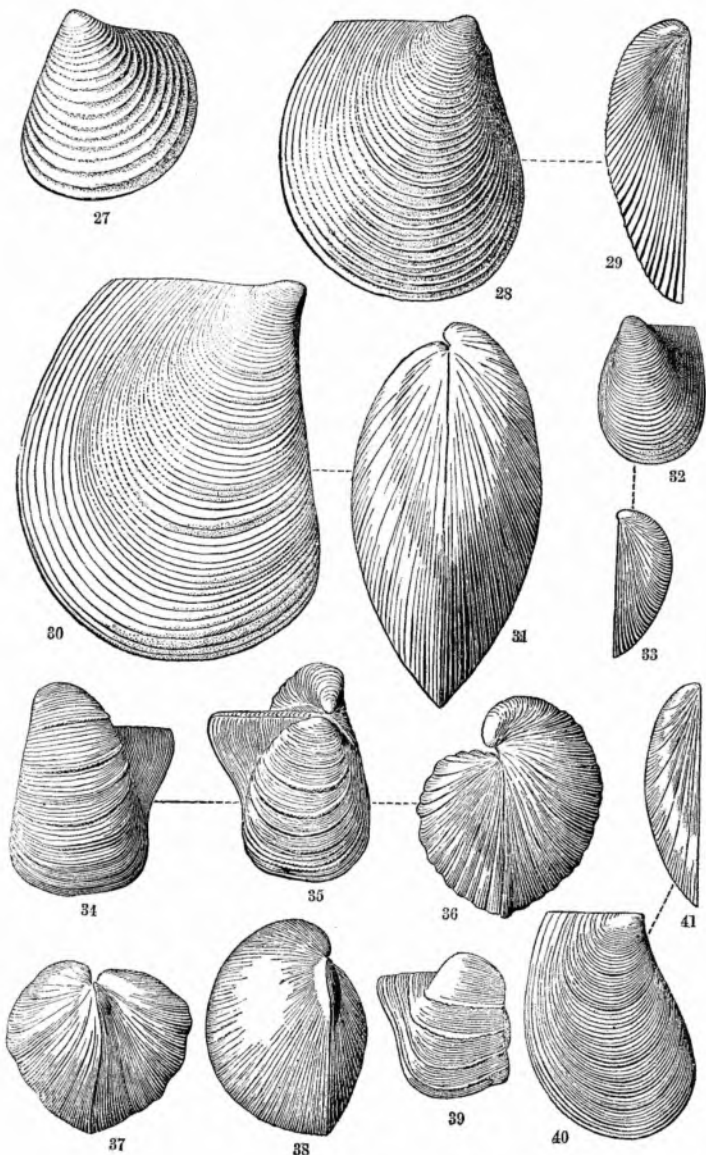
¹ H. Woods, *op. cit.* pl. xlix, figs. 5 & 6.

² *Id. ibid.* (1912) pl. liii, figs. 4-6.

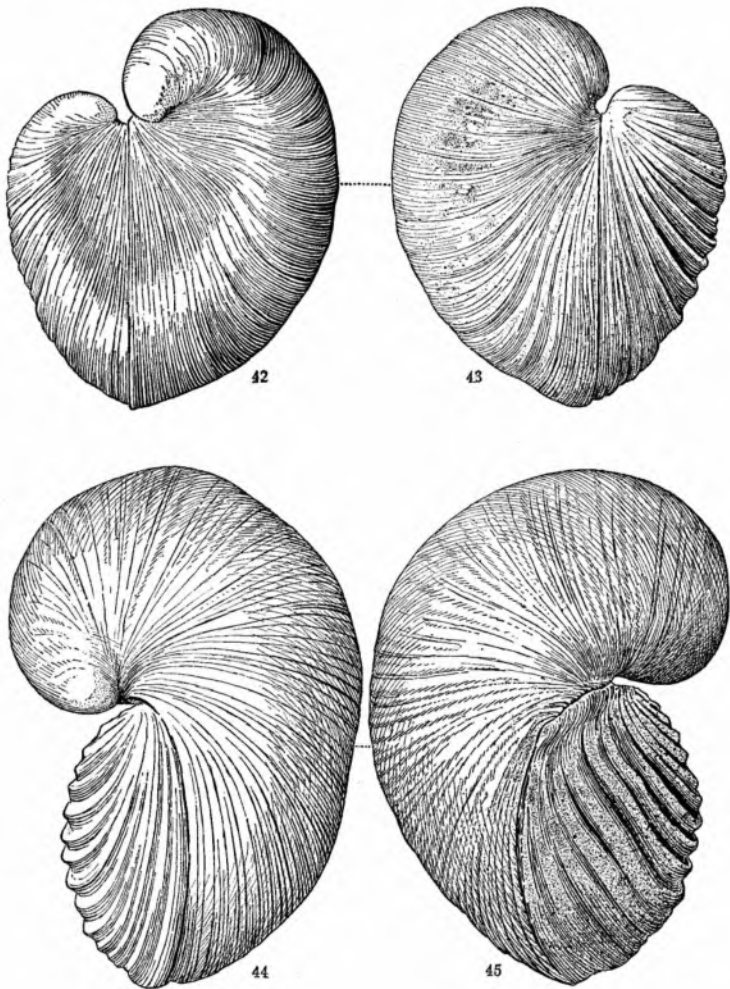
³ The resemblance is greater in the case of small forms of *I. pictus* than in the large example figured here.

⁴ *Id. ibid.* pl. liii, figs. 4-6, pl. liiii, figs. 1-7, & text-figs. 63-85.

⁵ *Id. ibid.* text-figs. 73-84.



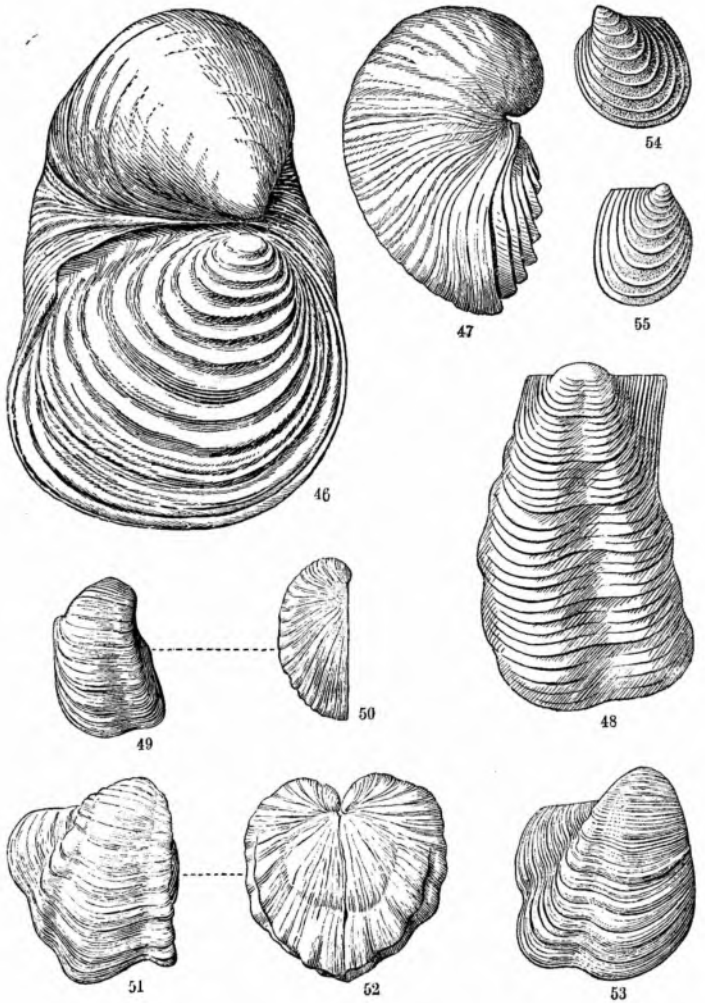
Figs. 27. *I. neocomiensis* d'Orb., Lower Greensand (Aptian): left valve. 28 & 29. *I. anglicus* Woods, Red Chalk: 28, right valve; 29, anterior. 30 & 31. *I. pictus* Sow., *Holaster-subglobosus* Zone: 30, right valve; 31, anterior. 32 & 33. *I. lamarcki* var. *apicalis* Woods, *Rhynchonella-cuvieri* Zone: 32, left valve; 33, anterior. 34-38. *I. lamarcki* Park., *Holaster-planus* Zone: 34, left valve; 35, right valve; 36, anterior; 37, 38, posterior. 39. *I. lamarcki* var. *websteri* Mant., *Micraster-cortudinarium* Zone: right valve. 40 & 41. *I. lamarcki* var. *cuvieri* Sow., *Terebratulina-lata* Zone: 40, right valve; 41, anterior. All @ half of the natural size.



Figs. 42 & 43. *Inoceramus* connecting *I. lamarcki* with *I. involutus*, Upper Chalk : 42, anterior ; 43, posterior. 44 & 45. *I. involutus* Sow., *Micraster cor-anguinum* Zone : 44, anterior ; 45, posterior. All @ half of the natural size.

anterior area which at first became concave and then decreased in size, ultimately disappearing (figs. 44 & 46). The right valve, in some forms of *I. involutus*, is moderately convex, with strong folds and a concave anterior area, and agrees with the right valve of one variety of *I. lamarcki*¹; in other forms which have departed farther

¹ H. Woods, *op. cit.*, p. 325 & text-fig. 85.



Figs. 46 & 47. *I. involutus* Sow., *Micraster cor-anguinum* Zone: 46, right valve and umbonal part of the left valve; 47, posterior view. 48. *I. lezennensis* Décoq, *Micraster cor-anguinum* Zone: right valve. 49 & 50. *I. lamarcki*; variety connecting *I. lamarcki* with *I. cordatus*, *Holaster-planus* Zone: 49, right valve; 50, anterior. 51-53. *I. cordiformis* Sow., *Micraster cor-anguinum* Zone: 51, 53, right valves; 52, anterior. 54 & 55. *I. costellatus* Woods, Chalk Rock: 54, left valve; 55, right valve. All @ half of the natural size.

from the *lamarcki* type, this valve becomes nearly flat (fig. 47, p. 10), the anterior area is lost, and the concentric folds increase in strength; the height of the shell decreases, and is often exceeded by the length.

From the large size and great thickness of the shell, and from the great difference in the form and size of the two valves, it seems evident that the characters which distinguish *I. involutus* from *I. lamarcki* were developed by the adoption of a more sedentary mode of life in which the animal rested on its left valve. The opercular character of the right valve, due to its decreased convexity and to the marginal growth around the hinge,¹ is in accordance with this view. Reasons for the short zonal range of *I. involutus* may be seen in the great size and thickness of the shell and in its specialized character.

I. involutus has been placed by Stoliczka and some later writers in a separate genus or subgenus—*Volviceramus*; but, since that species has been shown to have descended from *I. lamarcki*, the separation which would be implied by the use of the name *Volviceramus* can no longer be maintained.

I. cordiformis Sow. (figs. 51–53, p. 10) is found in the zones of *Micraster cor-testudinarius* and *M. cor-anguinum*, and in the *Uintacrinus* Band of the zone of *Marsupites testudinarius*, also possibly in an earlier zone. It has been derived from an inflated form of *I. lamarcki* with nearly equal valves, with which it is connected by an intermediate variety (figs. 49 & 50). It differs from *I. lamarcki* in the equal size of the valves, the relatively longer hinge, the presence of a radial sulcus extending from behind the umbo to the postero-ventral extremity, and often also of another sulcus from the front of the umbo to the opposite ventral margin; when this sulcus is present the large anterior area is limited by a rounded ridge. In one variety of *I. lamarcki* (figs. 49 & 50) this anterior sulcus is found, but the shell is shorter than in *I. cordiformis*.

I. costellatus Woods (figs. 54 & 55, p. 10) is found only in the Chalk Rock (zone of *Heteroceras reussianum*), and has probably been derived from *I. lamarcki* var. *apicalis* by the axis of growth becoming more oblique to the hinge, accompanied by the development of a narrower and more prominent left umbo.

I. subcardissoides Schlüt.,² *I. digitatus* Sow.,³ *I. pinniformis* Will.,⁴ and *I. corrugatus* Woods,⁵ from the Upper Chalk, are allied to one another and possess strong radial folds. No perfect specimen of these species showing the umbo and hinge has yet been found; but, from the character of the posterior ear and the curvature of the concentric folds, it seems probable that they have been derived from

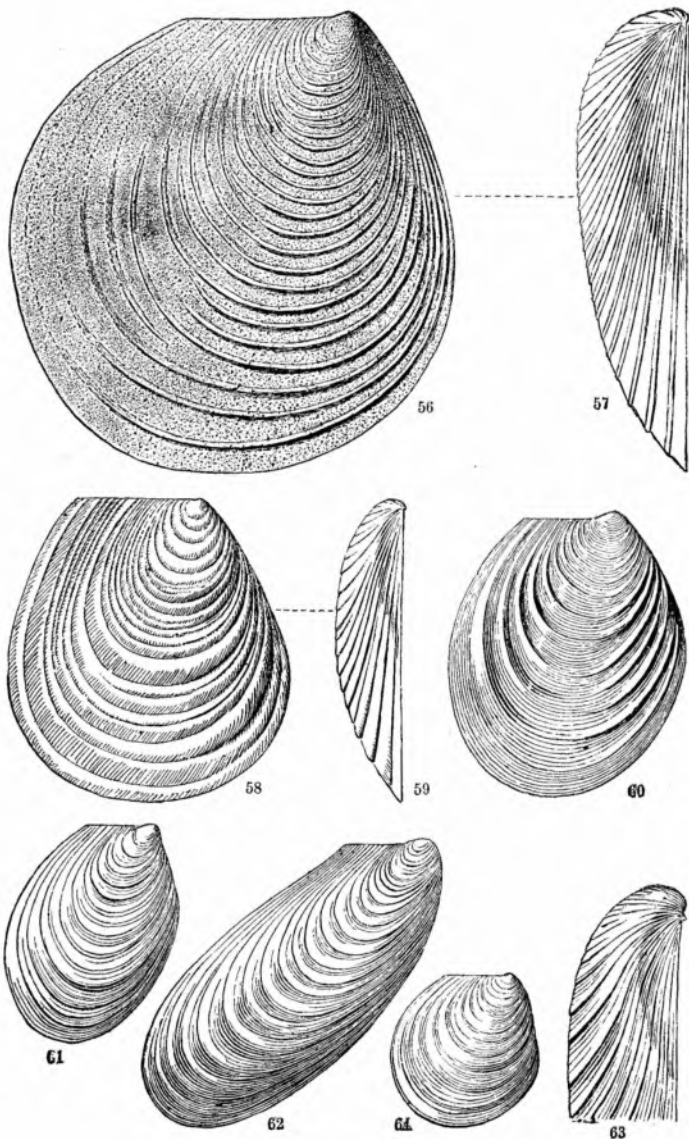
¹ H. Woods, *op. cit.* fig. 94.

² Palæontographica, vol. xxiv (1877) p. 271 & pl. xxxvii.

³ H. Woods, *op. cit.* text-fig. 95.

⁴ *Id. ibid.* text-fig. 96.

⁵ *Id. ibid.* text-fig. 97.



Figs. 56 & 57. *I. anglicus* Woods, Red Chalk : 56, right valve ; 57, anterior. 58 & 59. *I. crippsi* Mant., *Pecten-asper* Zone : 58, right valve ; 59, anterior. 60. *I. crippsi* var. *reachensis* Eth., *Holaster-subglobosus* Zone ; right valve. 61-63. *I. labiatus* Schloth., *Rhynchonella-cuvieri* Zone : 61, right valve of incompletely-grown individual ; 62, right valve of fully-grown individual ; 63, anterior view of part of right valve. 64. *I. labiatus* var. *latus* Sow., *Holaster-planus* Zone ; right valve. All @ half of the natural size, except fig. 62, which is a third of the natural size.

the less convex forms of *I. lamurcki* with concentric folds. That radial folds or corrugations, which give greater strength to the shell, can be developed in that stock is shown by the occasional presence of a fold in *I. lamurcki*, by the folds in *I. cordiformis*, and still more by the fold in *I. lezennensis* Décocq¹ (fig. 48, p. 10).

I. crippi Mant. (figs. 58 & 59, p. 12)² ranges from the Upper Greensand to the zone of *Holaster subglobosus*. It appears to have been derived from the forms of *I. anglicus* which possess fewer and less regular ribs (figs. 56 & 57). It agrees in many respects with *I. anglicus*, but the shell is relatively shorter, the part of the valve between the umbo and the ventral margin is less convex (so that the postero-dorsal part of the shell is relatively less compressed), and the anterior area is smaller; the ribs are fewer, more irregular, and their posterior curvature towards the hinge-line is less strong. In *I. crippi* var. *reachensis* Eth. (fig. 60),³ ranging from the Chalk Marl (*varians* zone) to the zone of *Holaster subglobosus*, the shell, when fully grown, is relatively higher, and the posterior curvature of the ribs is greater than in *I. crippi*.

I. labiatus (Schloth.) (figs. 61-63, p. 12)⁴ is found commonly in the zone of *Rhynchonella cuvieri*, and also occurs in the zone of *Terebratulina lata*. The curvature of the ribs, the similarity of the anterior area, and the fact that the anterior margin of the shell is at first perpendicular to the hinge,⁵ make it most probable that this species has descended from *I. crippi* var. *reachensis*. The main differences which appear in *I. labiatus* are due to the extensive growth of the shell in a direction oblique to the hinge-line, so that in fully-grown specimens (fig. 62) the form appears very different from that of *I. crippi*. On account of this mode of growth, the resemblance between small specimens of *I. labiatus* (fig. 61) and the adult of *I. crippi* var. *reachensis* is greater than in older specimens. Unfortunately, but few perfect specimens of *I. crippi* and its variety *reachensis* have yet been found, so that their variation cannot be studied satisfactorily; and no forms intermediate between this species and *I. labiatus* have been seen.

I. labiatus var. *latus* Sow. (fig. 64, p. 12)⁶ occurs in the zone of *Holaster planus*. The specimens of *I. labiatus* found in the zone of *Terebratulina lata* are often relatively longer and less high than the examples which occur in the zone of *Rhynchonella cuvieri*, and such forms pass gradually into *I. labiatus* var. *latus*, in which the length of the hinge-line has increased in proportion to the height of the shell; the axis of growth has become less oblique, the anterior margin more convex, and the ventral margin less sharply curved.

¹ C. Barrois, Ann. Soc. Géol. Nord, vol. vi (1879) p. 455 & pl. v, figs. 1-2.

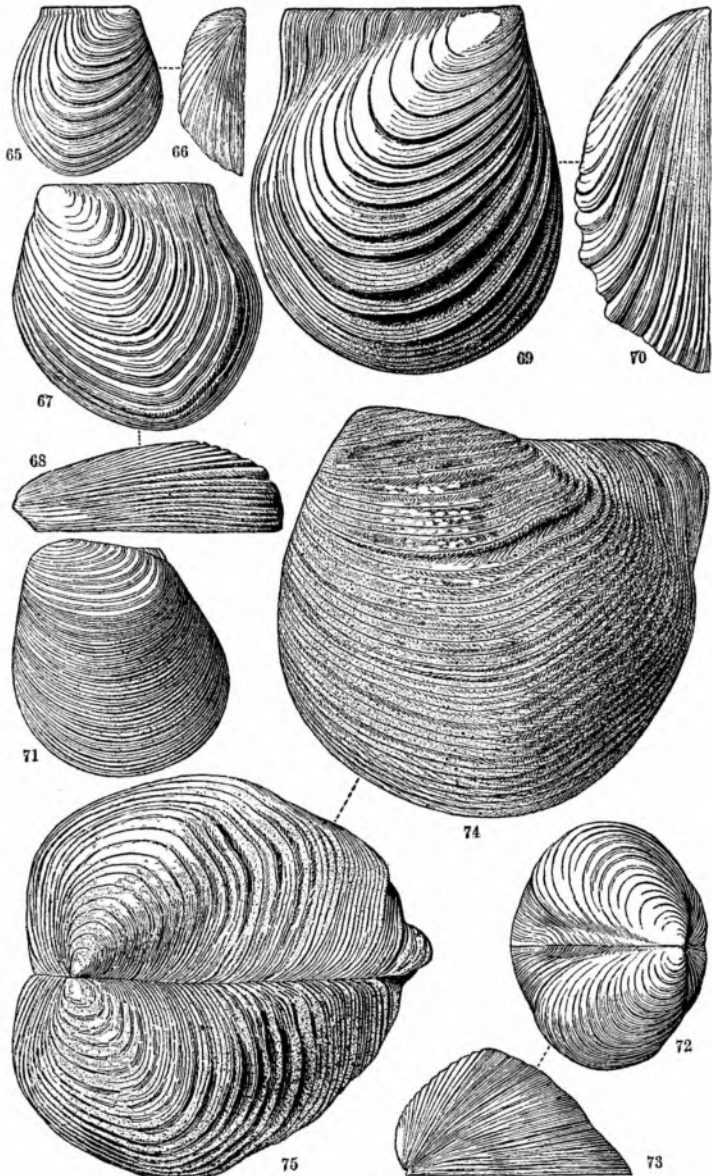
² H. Woods, *op. cit.* pl. xliii, figs. 2-3 & text-figs. 33-35.

³ *Id. ibid.* pl. xlvi, figs. 4-5 & pl. xlix, fig. 1.

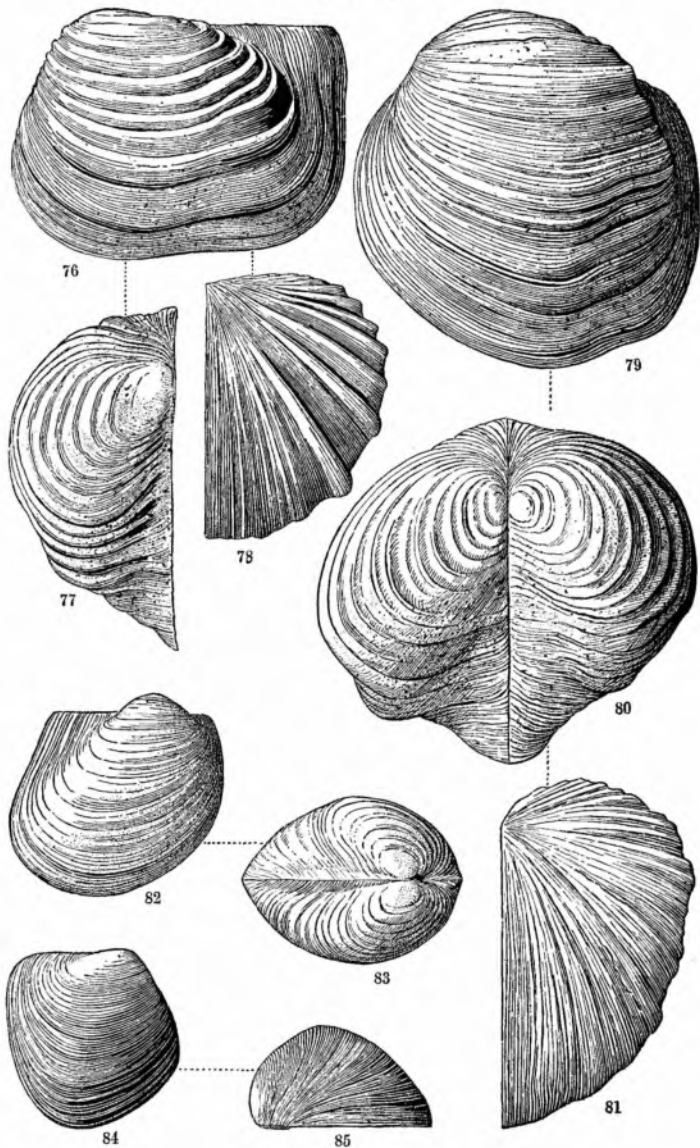
⁴ *Id. ibid.* pl. l & text-fig. 37.

⁵ *Id. ibid.* pl. l, fig. 4.

⁶ *Id. ibid.* text-figs. 38, 40, & 41 (*non* 39).



Figs. 65-75. *I. inconstans* Woods : 65-68, 71-73, *Holaster-planus* Zone ; 69 & 70, *Actinocamax-quadratus* Zone ; 74 & 75, Upper Clalk ; 65, 69, right valves ; 67, 71, 74, left valves ; 66, 68, 70, anterior views ; 72, dorsal view of 71 ; 75, dorsal view of 74. All @ half of the natural size.



Figs. 76-81. *I. inconstans* Woods, *Actinocamax-quadratus* Zone : 76, left valve ; 77, dorsal view of 76 ; 78, anterior ; 79-81, inflated form connecting *I. inconstans* with *I. inconstans* var. *sarumensis* ; 79, left valve ; 80, dorsal view of 79 ; 81, anterior. 82 & 83. *I. inconstans* var. *sarumensis* Woods, *Actinocamax-quadratus* Zone : 82, right valve ; 83, dorsal. 84 & 85. *I. inconstans* var. *striatus* Mant., *Holaster-planus* Zone : 84, right valve ; 85, posterior. All @ half of the natural size.

I. inconstans Woods (figs. 65-80 & 86, pp. 14-15 & 17)¹ extends from the zone of *Holaster planus* to the zone of *Belemnitella mucronata*, and perhaps occurs also in the zone of *Terebratulina lata*. It shows a large amount of variation. The less convex forms of this species approach very closely *I. labiatus* var. *latus*; but the hinge usually is relatively longer, the height of the shell less, the axis of growth more oblique to the hinge, the flattened area larger, the umbones less prominent, and the posterior ear more distinct. *I. inconstans* has undoubtedly been derived from the *labiatus* stock, and came probably from *I. labiatus* var. *latus*, but possibly from the longer and less high form of *I. labiatus* which occurs in the zone of *Rhynchonella cuvieri*.

From the variety of *I. inconstans* which throughout life is nearly flat or but slightly convex (fig. 67, p. 14), numerous varieties have arisen in which, sooner or later, the shell becomes convex or inflated owing to the later part growing towards the plane of the valves instead of nearly parallel to it: consequently the later-formed part curves more or less rapidly from the earlier part. The flat stage may last for a long (fig. 67) or a short period (figs. 71, 74), and in one variety (*sarumensis*, found in the *Actinocamax-quadratus* Zone, figs. 82 & 83, p. 15) disappears altogether, with the result that a regularly convex shell, without folds, is formed. Sometimes the change from the flat to the convex stage is abrupt, so that a sharp bend in the shell occurs (figs. 71-73, p. 14); in other cases, the change is gradual, and a dorso-ventral section of the shell is convex (figs. 74 & 75). When the flat stage is of short duration, the anterior flattened area becomes relatively shorter, and in the variety *sarumensis* (figs. 82 & 83, p. 15), in which the flat stage is lost, the anterior area is absent, and the umbo is not terminal.

I. inconstans var. *striatus* Mant. (figs. 84 & 85, p. 15),² found in the zones of *Holaster planus* and *Micraster cor-anguinum*, is another form in which the flat stage is absent; the valves are inflated, the folds indistinct, and the anterior area absent or indistinct.

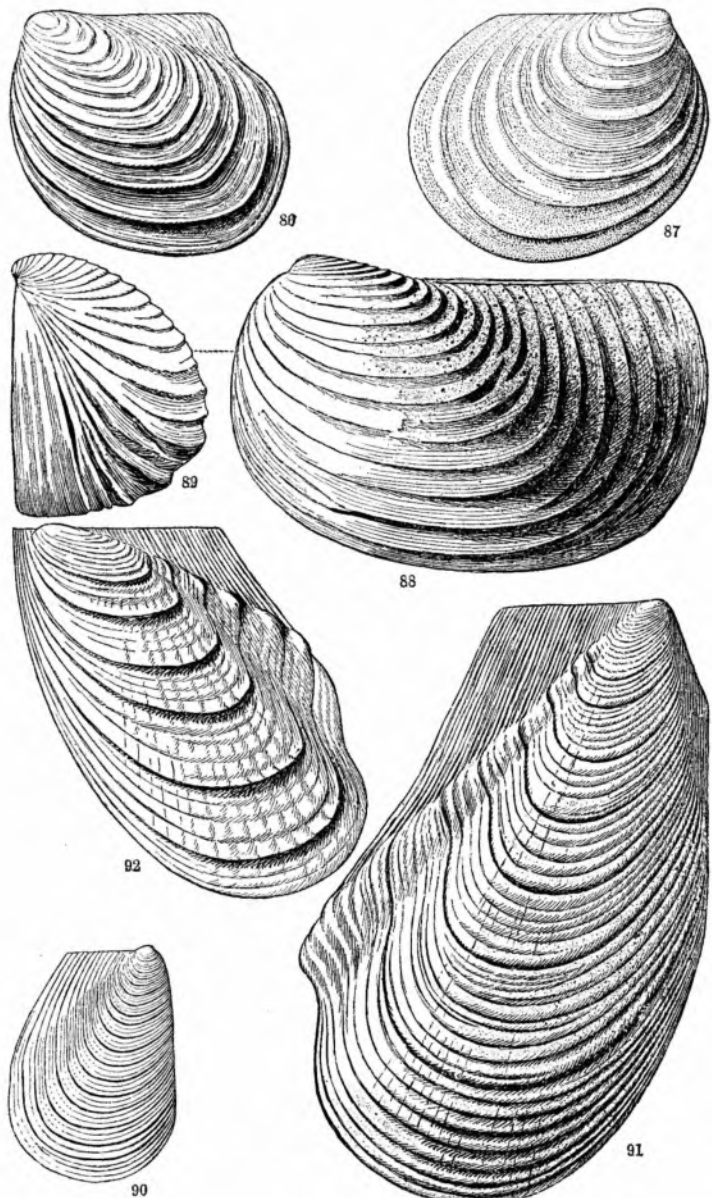
I. balticus Böhm (figs. 87-89, p. 17)³ ranges from the zone of *Marsupites testudinarius* to the zone of *Belemnitella mucronata*. In some examples of the slightly convex form of *I. inconstans* the hinge is relatively longer than usual (fig. 86), and these approach very closely the shorter and less convex forms of *I. balticus* (fig. 87) and also resemble the early stage of the large, convex form.⁴ Other examples of *I. balticus* (especially older individuals) are much longer, and the axis of growth becomes more oblique to the hinge-line; the valves become much more convex, owing to the change in the mode of growth like that already described in *I. inconstans*. It seems clear that *I. balticus* has been derived from *I. inconstans* by an increase in the relative length of the shell.

¹ H. Woods, *op. cit.* pl. li, figs. 1-4 & text-figs. 39, 42-49.

² *Id. ibid.* pl. li, fig. 5 & pl. lii, fig. 1.

³ *Id. ibid.* text-figs. 51-53.

⁴ *Id. ibid.* text-fig. 53.



Figs. 86. *I. inconstans*, elongate form, Upper Chalk; left valve. 87-89. *I. balticus* Böhm, Upper Chalk: 87, right valve of slightly convex form; 88 & 89, left valve and anterior view of fully-grown convex form. 90. *I. lingua* Goldf., Upper Chalk: right valve. 91. *I. lobatus* Goldf., *Actinocamax-quadratus* Zone. 92. *I. cardissoides* Goldf., *A.-g.* Zone; left valve. All @ half of the natural size.

The 'genera' *Endocostea* Whitfield¹ and *Haenleinia* Böhm² have almost certainly been derived from *I. balticus* and should, I think, be included in the genus *Inoceramus*.

I. lingua Goldf. (fig. 90, p. 17),³ from the zones of *Marsupites testudinarius*, *Actinocamax quadratus*, and *Belemnitella mucronata*, also appears to have descended from the flat form of *I. inconstans*, which it resembles closely. The principal differences seen in *I. lingua* are the greater relative height of the shell, giving more acute umbones, the rather less convex valves and consequently smaller anterior area. In *I. lingua* the flat stage appears to have continued throughout life.

I. lobatus Goldf. (fig. 91, p. 17),⁴ from the zones of *Marsupites testudinarius* and *Actinocamax quadratus*, is very closely allied to *I. lingua*; but in it an angular ridge or carina between the umbo and the postero-ventral extremity has been developed, and in front of this is a sulcus: the ridge gives a definite line of separation to the posterior ear, and the sulcus causes the ribs to become sinuous. A further difference from *I. lingua* is generally seen in the more distinct differentiation of the ribs into two sizes.

I. cardissoides Goldf. (fig. 92, p. 17),⁵ from the Upper Chalk (probably zone of *Actinocamax quadratus*), is closely related to *I. lobatus*; but radial ribs have been developed, and the concentric ribs have become stronger.

I. tuberculatus Woods (fig. 93, p. 19),⁶ from the zone of *Actinocamax quadratus*, possesses the main characters of *I. lobatus* and *I. cardissoides*. It appears to have arisen from the former by the development of radial ribs which, in combination with the concentric ribs, give a tuberculate type of ornamentation.

I. undulato-plicatus Röm. (fig. 94, p. 19),⁷ from the Upper Chalk, is of the same type as the flat forms of *I. inconstans*, especially in its early stages where concentric ribs only are present; but subsequently diverging radial ribs are developed. Although no connecting-forms have been found, it seems probable that this species has descended either from *I. inconstans* or from some closely related form.

¹ 'Prelim. Rep. Paleont. Black Hills' (Powell's Geol. & Geogr. Surv. Rocky Mt. Region, 1877) p. 31; and 'Paleont. Black Hills of Dakota' (U.S. Geol. & Geogr. Surv. Rocky Mt. Region, 1880) p. 402. See also A. d'Orbigny, 'Pal. Franç.: Terr. Crét.' vol. iii (1846) p. 515 & pl. cccix; II. E. Beyrieh, Zeitschr. Deutsch. Geol. Gesellsch. vol. iv (1852) p. 151 & pl. v; & J. Böhm, Abhandl. d. k. Preuss. Geol. Landesanst. n. s. pt. lvi (1909) p. 48.

² J. Böhm, *ibid.* (1909) pp. 53-58 & pls. xiii-xiv.

³ H. Woods, *op. cit.* text-fig. 56.

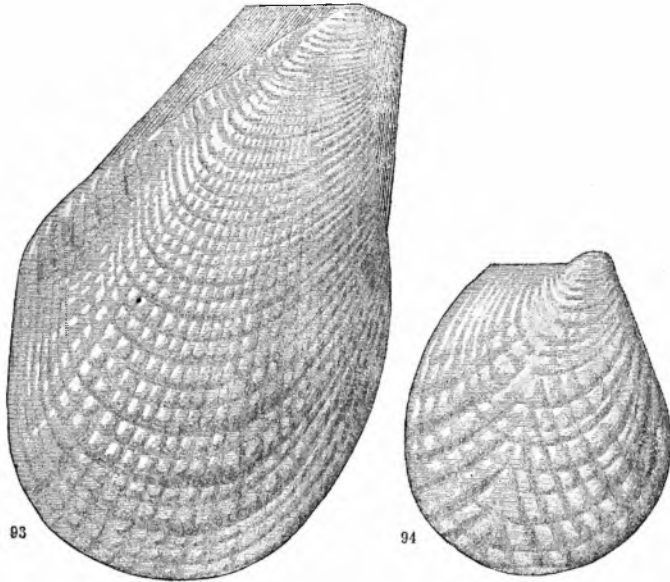
⁴ *Id. ibid.* text-figs. 54 & 55.

⁵ *Id. ibid.* text-figs. 57 & 58.

⁶ *Id. ibid.* pl. liv, fig. 8 & text-fig. 59.

⁷ *Id. ibid.* text-figs. 60 & 61.

I. undulato-plicatus var. *digitatus* Schlüt.¹ has the posterior ribs more strongly developed than in *I. undulato-plicatus*.



Figs. 93. *I. tuberculatus* Woods, *Actinocamax-quadratus* Zone; right valve.
94. *I. undulato-plicatus* Röm., Upper Chalk; right valve. Half of the natural size.

It is interesting to note that radial folds have been developed independently in several groups of Cretaceous *Inocerami*, namely: (1) *I. concentricus* var. *subsulcatus*, *I. sulcatus*; (2) *I. cordiformis*; (3) *I. subcardissoides*, *I. digitatus*, *I. pinniformis*, *I. corrugatus*; (4) *I. cardissoides*, *I. tuberculatus*; and (5) *I. undulato-plicatus*.

In conclusion, I wish to express my thanks to Dr. H. P. Blackmore, Mr. R. M. Brydone, Mr. C. P. Chatwin, Mr. G. E. Dibley, Mr. W. Hill, Dr. A. W. Rowe, and Mr. C. D. Sherborn for the loan of numerous specimens, without which this paper could not have been written. I am also indebted to Mr. C. P. Chatwin for placing his extensive knowledge of the zonal distribution of the Chalk *Inocerami* at my disposal, and for help in other ways.

The figures illustrating this paper have been drawn by Mr. T. A. Brock.

¹ Palæontographica, vol. xxiv (1877) p. 267 & pl. xxxvi.
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