INTRASPECIFIC VARIATION IN, AND ONTOGENY OF, *PRIONOTROPIS WOOLLGARI* AND *PRIONOCYCLUS WYOMINGENSIS*

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INTRODUCTION

WHILE SIFTING THE AMMONITE COLLECTIONS of the American Museum of Natural History, the writer was fascinated by the fact that specimens from various parts of the western interior roughly referable to *Prionocyclus wyomingensis* deviated in some respects from Meek's types of this species, as figured by White, by the unusually good preservation of some of these specimens and by the morphological contrasts between early and late ontogenetic stages occurring in some Prionotropidae, particularly in *Prionocyclus* and even more so in *Prionotropis*.

Earlier plans for this study, suggested by these observations, were given a further impulse by the fact that the fragment I described and figured some time ago (Haas, 1943) from Mount Taylor country, New Mexico, as a presumably Albian ammonite under the name "*Pervinquieria* cf. *romeri* Haas" turned out to belong to an adult *Prionocyclus*, closely comparable to *P. wyomingensis*. This fact, of course, invalidates also the stratigraphic and paleogeographic inferences drawn in that article.[1] I am deeply indebted to Dr. John B. Reeside, Jr., of the United States National Museum for drawing my attention to the fact that Prionotropidae identical with, or at least very similar to, the fragment mentioned above had been previously collected by Dr. T. W. Stanton and by Mr. C. B. Hunt from strata belonging undoubtedly to the Upper Cretaceous Mancos shale of the same region.

The great ontogenetic changes occurring particularly in *Ammonites woollgari* have been noticed and emphasized by students of this species almost since its creation by Mantell in 1822. As early as 1829 Sowerby (p. 165) wrote: "The central whorls of this fossil, separated and compared with the external one, would never be thought the same species." The next author to deal with Mantell's species, Sharpe, made the following statement in 1854 (p. 27): "There is hardly any species of Ammonite which undergoes so great a metamorphosis as *A. woollgari*." Also De Grossouvre (1893) in his introduction (p. 7) cites this species as a striking example of ontogenetic changes in ammonites: "Qui pourrait reconnaître, par exemple, au premier coup d'oeil, le jeune d'Ammonites Woolgari (Sharpe, Fossil Molluska of the Chalk, pl. 11, fig. 1) dans l'échantillon représenté même planche, fig. 2?" However, the reader of this report will certainly agree with its writer that the contrasts between various ontogenetic stages of *Ammonites woollgari* known to the authors just quoted are considerably less striking than those prevailing, for example, between the specimen depicted in Hall and Meek's (1855) plate 4, figure 2a, and that shown in plate 14, figure 11, of this paper, both of which are here referred to *Prionotropis woollgari* Meek, or between the earlier stages of its var. *praecox*, as seen in plate 16, figures 22–27, and the holotype and the largest paratype of this variety, shown in plate 17.

It is, however, not only these great ontogenetic changes that account for the extreme variability of the morphologic aspects displayed by different individuals of the two species here dealt with, but also a wide range of intraspecific variation. The latter, in its turn, is due, especially in *Prionotropis woollgari*, to a large extent to differences in the speed of development, as certain phases of ornamentation appear earlier or persist longer in one form than in another. Thus comes about an almost bewildering abundance of forms which may differ widely from one another even at the same growth stages. Intergradations between these various forms are found in both species, and merely varietal significance is therefore assigned to the differences between them. The species themselves may be considered truly "grandes espèces" according to Depéret (1907, p. 142) or, to use a more modern term, polytypic species.[2] I am fully aware of the fact that

[1] It appears only fair to point out that I am solely responsible for that misidentification and that Prof. Gayle Scott's comments, quoted in that article (Haas, 1943, pp. 2–3), were based on my communication that a "horned" *Pervinquieria* of apparently Albian age had been found in Mount Taylor country.

[2] The troubles facing the taxonomist dealing with materials of this kind are clearly pointed out and remedies against them are recommended in a recent paper on

some, if not all, of the various forms here included in *Prionotropis woollgari, sensu lato*, particularly if collected from different localities and described singly, might by many an ammonitologist be referred to as many different species, if not subgenera. The present report, however, endeavors to demonstrate how the trend toward splitting is bound to increase in direct proportion to the scarcity of the material available.

Since most of the various forms distinguished within either species occur, both stratigraphically and topographically, associated with each other (see, for *Prionotropis woollgari*, the block figured in pls. 11, 12, and pl. 24, fig. 1), they are considered varieties of the typical form but not subspecies (cf. Haas, 1942c, p. 207, footnote 1).[1]

To the interaction of this high degree of intraspecific variation on the one hand and the thorough ontogenetic changes on the other is due the truly perplexing variety of morphologic aspects described in the following pages and shown in the accompanying illustrations. For both species here dealt with the synonymy is discussed, and an attempt is made to find out the typical form, then to establish the varieties clearly distinguishable from it and to select type specimens for the typical forms as well as for the newly established varieties. Then the ontogeny of both species is discussed as to dimensions, estimated length of body chamber and size attained, whorl section, ornamentation, and suture lines, always differentiating between the various forms distinguished within the species and, in the case of *Prionocyclus wyomingensis*, dealing by way of appendix with a few specimens *incertae sedis* but doubtfully referable, or at least closely comparable, to that species.

A thorough study of the ontogeny of the two species under discussion, combined with a careful redescription of their various types and illustrated by adequate figures, seems to be the more desirable since hardly anything essential has been added to knowledge of them since Meek's (1876) and White's (1880) early papers[2]; also, to quote Dr. Reeside (letter to the writer, dated April 13, 1943), "no one has published figures of the large adults of these genera and it is not surprising they go unrecognized." On the other hand, both *Prionotropis woollgari* and *Prionocyclus wyomingensis* are again and again quoted in literature; they are described and depicted as index fossils by Grabau and Shimer (1902, pp. 227, 228, figs. 1509a–d, 1510a–d) as well as by Shimer and Shrock (1944, p. 593, pl. 247, figs. 1–5) and are repeatedly (Reeside, 1924, p. 11, pl. 3; Moreman, 1927, pp. 91, 97; 1942, pp. 193, 194; Warren and Rutherford, 1928, pp. 132, 135; Muller and Schenck, 1943, p. 272, fig. 6) used as zone or subzone fossils.

In the present report the specimens referred to are as a rule quoted merely by their

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Dorset Lias Foraminifera by Macfadyen (1941, p. 6): "Certain authors have endeavoured to describe such . . . faunas by the multiplication of trivial names. By the nature of the problem these forms are generally ill-defined and insufficiently differentiated from neighbouring species both in nature and by their authors. A natural consequence of this is that the greater the number of such similar species that are proposed, the more do intermediate specimens become unnameable. . . .

It is preferable to subdivide these ill-defined aggregates of a population rather broadly, using few trivial names, and allowing considerable variation to each species. This view is supported by the variability which is found among a group of specimens in a single sample, so that neither peculiar geographical distribution nor time change can be cited in favour of splitting."

[1] No genetic significance is implied in this use of the term "variety." It rather serves as an expedient for the distinction of various forms believed to fall within the morphologic range of a polytypic species. They might be called "form A," "form B," etc., as well, but names are thought to serve the above purpose better than mere symbols and might, moreover, readily be converted into specific names, should later workers in this field prefer to assign species rank to one or another of these forms.

[2] It seems significant that of 10 papers dealing with *Prionotropis woollgari* after Meek (see synonymy, p. 150) three were restricted fully, or at least chiefly, to reprinting Meek's original description in full and to reproducing his figures; of the seven others only four published new figures and only three made some additions to the original description. Similarly, of five authors discussing *Prionocyclus wyomingensis* after White (see synonymy, p. 200) three merely reproduced his figures, one reprinted his description, but none except Stanton (1893) contributed anything of significance, be it by additional description or by new illustrations. In the above statistics authors describing forms here included in the synonymy of either of these species under other names have been left out of account, as have, for obvious reasons, Grabau and Shimer's (now Shimer and Shrock's) "North American index fossils" and Roman's monograph on Jurassic and Cretaceous ammonites.

museum numbers, with the following abbreviations:

A.M.N.H., American Museum of Natural History
C.N.H.M., Chicago Natural History Museum (formerly Field Museum of Natural History)
Col. Univ., Geological Department, Columbia University
S.D.S.S.M., South Dakota State School of Mines
U.N.S.M., University of Nebraska State Museum
U.S.N.M., United States National Museum

For the localities and horizons of the specimens thus quoted, reference is made to the sections "Material studied" (pp. 197, 215, respectively). Within the lots to which the museum numbers refer, individual specimens are designated by adding in the case of the American Museum of Natural History a subnumber preceded by a colon and, in all other cases, a lower case letter to the lot number.

I wish to express my gratitude to Dr. Reeside and to the authorities of the United States National Museum for permission to prepare and study numerous ammonites of that museum's collections and to describe and figure some of them in this report, and to Dr. Reeside in particular for valuable information on some of the type specimens of that museum; furthermore, to the following curators and institutions for permission to study and, as far as desirable, to publish specimens, including types, of their collections: Dr. H. W. Nichols, Chicago Natural History Museum; Prof. G. Marshall Kay, Department of Geology, Columbia University; Dr. J. D. Bump and Dr. J. P. Gries, South Dakota State School of Mines; Prof. M. K. Elias and Dr. C. B. Schultz, University of Nebraska State Museum. I am further indebted to Dr. Barnum Brown, former head of the Department of Paleontology of this Museum, for valuable oral information concerning the occurrence of the specimens which he collected in southwestern South Dakota 40 years ago, and to Prof. J. P. Gries of the South Dakota State School of Mines for a field sketch of the stratigraphy of a locality near Hot Springs, South Dakota, which yielded some of the specimens studied. Miss Helen Babbitt carried out, excellently as usual, the suture line and whorl section drawings accompanying this paper, and Mr. W. H. Southwick, staff artist of this Museum, devoted his expert skill and untiring patience to the preparation of the photographic plates.

Last but not least, I am greatly indebted to the Geological Society of America for a grant from the Penrose Bequest in support of the illustrations accompanying this report.

PRIONOTROPIS WOOLLGARI[1] MEEK (? *NON* MANTELL)

SYNONYMY

? *Ammonites Woollgari* MANTELL, 1822, p. 197, pl. 21, fig. 16, pl. 22, fig. 7.

? *Ammonites Woollgari;* SOWERBY, 1829, p. 165, pl. 587, fig. 1.

? *Ammonites Woollgari* Mantell; SHARPE, 1854, p. 27, pl. 11, figs. 1, 2.

Ammonites percarinatus HALL AND MEEK, 1855, p. 396, pl. 4, fig. 2.

Ammonites Graysonensis SHUMARD, 1857, p. 593.

Prionocyclus woolgari Mantell (sp.); MEEK, 1876, p. 455, pl. 6, fig. 2, pl. 7, figs. 1, 3.

Ammonites graysonensis Shumard; WHITE, 1880, p. 39, pl. 18, fig. 9.

Prionotropis woolgari Mantell (sp.); STANTON, 1893, p. 174, pl. 42, figs. 1–4.

Ammonites graysonensis; STANTON, 1893, pp. 48, 177.

? *Schloenbachia woolgari* Mantell; CRAGIN, 1893, p. 243.

Prionotropis woolgari Mantell; LOGAN, 1898, p. 466, pl. 102, figs. 1–4.

? *Prionotropis woolgari*—Meek; LOGAN, 1899, p. 211, pl. 24, figs. 1–6.

Prionocyclus woolgari Mantell; HERRICK AND JOHNSON, 1900, p. 215, pl. 2, fig. 1.

Prionotropis woolgari Mantell (sp.); JOHNSON, 1903, p. 141, pl. 12, fig. 31.

? *Prionotropis woolgari* Mantell; SHIMER AND BLODGETT, 1908, p. 66.

P. Woolgari (Mantell); GRABAU AND SHIMER, 1910, p. 227, fig. 1509a–d.

Prionotropis aff. *woolgari* (Mantell); MOREMAN, 1927, p. 97, pl. 13, fig. 1.

Prionotropis aff. *woolgari* Stanton 1893, . . . Meek, 1876 . . . ; ADKINS, 1928, p. 250.

? *Prionotropis graysonensis* (Shumard); ADKINS, 1928, p. 249.

Prionotropis Woolgari Mantell; ROMAN, 1938, pp. 455, 457, *pro parte;* pl. 46, fig. 434b, 434c.

Prionotropis aff. *woolgari* Meek (not Mantell); MOREMAN, 1942, p. 214.

Prionotropis graysonensis (Shumard); MOREMAN, 1942, p. 213.

P. woolgari (Mantell); SHIMER AND SHROCK, 1944, p. 593, pl. 247, figs. 1, 2.

Mere mentions of the species in faunal lists or otherwise in geological papers, unless accompanied by illustrations, have not been included in the synonymy.

With a reservation concerning the sutural characters, Meek (1876, p. 457, see also p. 453, footnote) believed his form from the Black Hills of Dakota and Mantell's from the Lower Chalk near Lewes, England, to be "really specifically identical." Stanton (1893, p. 175) discussed this issue, whereas in the three next decades or so other American students did not question Meek's above conception; but both De Grossouvre[2] and Pervinquière[3] did, though with typically French courtesy most cautiously. In modern times, however, such doubts were voiced, much more decidedly, by American authors also, as by Adkins (1928, p. 250)[2] to whom Meek's "species is doubtless not identical with that of Mantell," and by Moreman (1942, p. 214). In my opinion the conspecificity of Meek's form with Mantell's certainly remains doubtful. The similarity between Sharpe's (1854, pl. 11) figure 2 and Meek's (1876, pl. 7) figure 1c, d, is indeed so striking as to suggest full conspecificity, but this does not solve the problem, since the original of Sharpe's figure 2 is none of Mantell's type specimens and, moreover, comes from the Middle, not the Lower, Chalk near Lewes. The type of *Ammonites woollgari* Mantell is undoubtedly the specimen figured in his plate 21, figure 16, and refigured by both

[1] The above spelling (with two "l's") is the correct one, since Mantell (1822, p. 197) named his species "in honour of my esteemed friend, Thomas Woollgar, Esqu., of Lewes . . . ." This spelling was kept by Sowerby (1829, p. 165) and Sharpe (1854, p. 27). Meek (1876), however, omitted the second "l," and this misspelling was followed by almost all later authors on both sides of the Atlantic (also by De Grossouvre, 1893, p. 29, and Pervinquière, 1907, p. 250). Only quite recently Muller and Schenck (1943, p. 272, fig. 6) restored the correct rendition of this specific name.

It might be added that, despite the Recommendations to Article 36 of the Rules of Zoological Nomenclature, this diversity in spelling between Mantell and Meek could not even be utilized in the case, suspected by many modern authors, that their forms should prove to be not conspecific. Since Meek intended to refer his specimens to Mantell's species, his omission of the second "l" is merely an error of transcription, subject to rectification (Article 19 of the Rules).

[2] 1893, page 29: "Ce genre [*Prionotropis*] a été créé en 1876 par Meek pour *Ammonites Woolgari*, ou du moins pour une forme qu'il croit identique à cette espèce."

[3] 1907, page 250: "Le genre *Prionotropis* dont le type est *Amm. Woolgari* Mantell (ou du moins une forme voisine que Meek lui assimile) . . . ."

Sowerby (pl. 587, fig. 1) and Sharpe (pl. 11, fig. 1), by the latter author with "restorations" which seem to give the ammonite a stiff aspect entirely lacking in Sowerby's beautiful drawing. Both these figures, to judge by Sowerby's text, seem to show the specimen in natural size, whereas Mantell's protograph is somewhat reduced. If this type specimen is compared with Meek's (1876, pl. 7) figure 1g, representing about the same ontogenetic stage, the conspecificity may be doubted. The problem becomes even more difficult if the wide differences obtaining between the various stages of even the same individual are taken into account. In the writer's opinion it cannot be solved without careful comparison of both Mantell's and Meek's types, not feasible under present world conditions. Even after the war the study of the ontogeny and therefore a thorough comparison will be rendered difficult by the rarity of the English form, emphasized by Mantell, Sowerby, and Sharpe.

Should this future study prove the conspecificity of Meek's form with Mantell's species, then the specimens figured by Meek, or at least those of them that will be proved fully identical with Mantell's type, would have to be considered merely the American hypotypes of the English species. In the opposite case, however, the name of Meek's form would have to be changed to *Prionotropis percarinatus* (Hall and Meek), since the latter name, suppressed by Meek (1876, pp. 466, 457) as a synonymn of *P. woollgari*, would then have to be revived as the specific name of the American form.[1] Also in this case, however, the latter, but not the true *Ammonites woollgari* Mantell, would have to be considered the genotype (or subgenotype) of *Prionotropis* Meek, as explicitly stated for this case by Meek (1876, p. 453, footnote) himself, and supported by De Grossouvre (*loc. cit.*) and Adkins (1928, p. 249.)

INTRASPECIFIC VARIATION

The problem of how to organize the abundance of individuals referable to *P. woollgari, sensu lato*, that were examined in the course of this study (about 445) so as to approach a natural grouping as closely as possible became more intricate the more material came in for study. It may be truly said that almost every "wave" of incoming material changed the aspects of this problem. Most informative was a block crowded with fossils from the collections of the United States National Museum which is believed to have been collected by the Powell Survey in southern Utah, exact locality unknown. It might well be called a fossilized population sample. After permission had been received from the authorities of the United States National Museum, this block (shown in three different views in pl. 11, pl. 12, and pl. 24, fig. 1) was broken up. Although it measured only 16 cm. by 10 cm. by 5 cm., it yielded about 325 specimens (including fragments) of the species under discussion. In addition, it contained a small *Metoicoceras* whose specific identity could not be established, a fragment of an *Inoceramus*, and some minute shells of *Scaphites* and of an undetermined gastropod, and some microfossils. Except for a fragment of a single horn belonging to a disk

[1] Here it might be added that careful comparison of Shumard's original description and of his drawing, as published by White (*loc. cit. in syn.*), with Hall and Meek's types proves *Ammonites graysonensis* to be a synonym of *A. percarinatus*, as, alternatively, suspected by Stanton (1893, p. 177). The close affinity of his form to *A. percarinatus* did not escape Shumard; the differences thought by him to be distinctive turn out to be due merely to incidentals of size and preservation. Moreman (1942, p. 213) believes *P. graysonensis* (Shumard) to be an independent species; however, both the features thought by him to be distinctive of Shumard's species (the "shortness" of the whorls in proportion to the width and the "not so distinct" serration of the keel) are present in Hall and Meek's types of *Ammonites percarinatus* and in topotypes from their locality, all in the collections of the American Museum of Natural History, as well. It must not be forgotten that the specimen figured by Moreman (1927, pl. 13, fig. 1) and referred to in his recent paper measures only 13 mm. in diameter, thus corresponding to a very early stage, and that it can therefore not well be compared with Meek's (1876) figures, the smallest of which (pl. 7, fig. 1f) shows a more advanced stage (diameter 27 mm., about twice that of Moreman's characteristic specimen). Since *Ammonites graysonensis* is thus believed to be identical with *A. percarinatus*, both these names are here considered synonyms for the young of *P. woollgari* Meek; this was apparently also Moreman's conception in 1927.

whose diameter may well be estimated at about 250 mm., none of the specimens of *P. woollgari* found in this block exceeds 40 mm. in diameter.

Grouping the ammonites of this species by the degree of involution and by the character of ornamentation, particularly by the earlier or later loss of its original density, was eventually thought to be the best solution of the above problem. However, it necessitates neglect of the whorl thickness (ratio W:H) as a mark of distinction between the various forms, except for the varieties *crassa* (p. 153) and *branneri* (p. 154), both of which are distinguished among other characters by a whorl thickness considerably exceeding that of the typical form. In the other forms here distinguished there is a more or less wide range of variation as to this character, widest in the variety *intermedia* and only a little less wide in the typical form, both of which are the two commonest forms within the material studied. However, establishment of "sub-varieties" according to these differences in thickness appeared not only highly undesirable but also unnecessary, since there is almost uninterrupted intergradation between the thickest individuals and the thinnest ones, as seen from the following tables of dimensions.

In this part of the present report the typical form of *P. woollgari* Meek will have to be selected first; then the variety *crassa*, thicker than the former, will be briefly discussed. The three next varieties to be dealt with, *intermedia*, *regularis*, and *tenuicostata*, may be arranged, after the typical form, in a morphologic row according to the character of ornamentation which tends to be, at a given diameter,[1] denser and finer in the order of enumeration; the ribs and the denticulations of the keel get farther apart from each other at an ever later ontogenetic stage.

Furthermore, there is a clear trend toward increase in involution in the row: *forma typica*–var. *intermedia*–var. *tenuicostata*–var. *regularis*, the places of the two last varieties now being interchanged as compared to the previous order according to sculptural characters.

It is true that the differences pointed out above are of a more or less quantitative character; accordingly, there is plenty of intergradation to be found between them. However, these quantitative differences add up to quite considerable amounts if the end links of the resulting morphological rows are compared with each other, e.g., plate 13, figure 9, with plate 16, figure 5, or with plate 16, figure 19; or plate 13, figures 14, 15, with plate 16, figure 10. Furthermore, a comparison of the ventral views of the lectotype of the *forma typica* (Meek, 1876, pl. 7, fig. 1b), of the largest specimen present of the variety *intermedia* (pl. 14, fig. 16), and of the holotype of the variety *regularis* (pl. 16, fig. 14), all three of these specimens measuring about 65 mm. in diameter, may well serve to illustrate the differences on which the distinction of various forms within this species has been based.

Apart from the morphologic series hitherto discussed the two last varieties, *praecox* and *alata*, will have to be dealt with.

(A) Forma typica

Plate 13, figures 1, 4–19, plate 14, figure 11; text figures 3–5, 25–29, 31–38

As pointed out by Adkins (1928, p. 249),[2] none of the specimens originally figured in 1876 by Meek has yet been designated as the type of the American form, should it turn out to be an independent species. Meek (1876, pp. 456–457) emphasizes that the ontogenetic changes occurring in his form "are not at any point abrupt, but that the peculiarities of one stage of development pass gradually into those of the next"; however, at least varietal differences seem to be recognizable within his type material. The best way of definitely clearing up the questions involved would, of course, be its careful reëxamination which is, however, impossible at present, the types of the United States National Museum having been stored for the duration of the war. Meanwhile the indi-

[1] In forms undergoing as rapid ontogenetic changes as the present ones, all comparisons must be based on a definite ontogenetic stage, as represented by a certain size. In the material examined the best opportunities for comparisons are found in disks averaging about 30 mm. in diameter; most of the respective statements thus refer to the stage between the diameters of 20 and 40 mm.

[2] That author's omission in this reference of Meek's figure 2, plate 6, is obviously erroneous.

vidual listed, among others, in the United States National Museum catalogue under No. 223 and illustrated by Meek's (1876, pl. 7) figure 1a, b (reproduced in Shimer and Shrock, 1944, pl. 247, figs. 1, 2) is here designated lectotype of the typical *Prionotropis woollgari* Meek (? *non* Mantell). The specimen shown in figure 1c, d, of the same plate is here referred to the new variety *intermedia*, as are several examples in the present material closely resembling this figure. Figure 1f is also referred to this variety. The specimen depicted in figure 2 of plate 6 and in figure 1g, h, of plate 7[1] is here designated the holotype of the variety *alata*, new name. The original of figure 3 on the same plate,[2] called in Meek's explanation of this plate "a fragment of non-septate part of an adult specimen, apparently of this species," remains doubtful as to its taxonomic position within the species, as long as its lateral aspect cannot be examined. Nor can Meek's specimen from which the suture line depicted in figure 1e of his plate 7 is taken properly be assigned to any of the forms here distinguished, pending the examination of the specimen itself.

The exact taxonomic position of Hall and Meek's (1854, pl. 4, fig. 2a, 2b) types of *Ammonites percarinatus* as well as of several topotypes (all of these specimens comprised under A.M.N.H. No. 9530/1), is difficult to ascertain, since none of them exceeds 25 mm. in diameter, and almost all of them are crushed. They might represent early growth stages of the variety *regularis* or may be of the variety *intermedia* rather than of the typical form.

The overwhelming majority of all the specimens here referred to the *forma typica*, found in the above-mentioned block as well as in various localities of South Dakota and Wyoming (U.S.N.M. Nos. 103895, 103894, 103907, 103914), measure less than 40 mm. in diameter. Only one (latex cast of a natural mold, U.S.N.M. No. 9083) from the glacial drift of Iowa corresponds in size to the lectotype designated above. A true medium size, corresponding to a diameter of about 125 mm., is represented by a very incomplete and worn specimen from near Newcastle, Wyoming (U.S.N.M. No. 103907a). The beautiful though short whorl fragment (C.N.H.M. No. P5932) whose suture lines were figured by Logan (1899, pl. 24, fig. 2; cf. pl. 13, figs. 4, 19, and text figs. 5 and 45 of this paper) and which is believed to be referable to the typical form belongs to a somewhat larger disk. Three giant conchs with imposing tubercles from the vicinity of Edgemont, South Dakota (A.M.N.H. No. 25986), the largest of which is preserved up to the apertural margin and attains a diameter of about 355 mm. (pl. 14, fig. 11), are, though doubtfully, also referred to the typical form. The fragment of a single horn, mentioned above to have been found in the block from southern Utah (attached to a specimen of the variety *regularis*, U.S.N.M. No. 103897k), might belong to a large disk of the typical form as well as of the variety *alata*.

(B) Var. **crassa**, new variety

Plate 14, figures 1, 5, plate 15, figures 7, 8; text figures 6, 39

Using the typical form, as established above, as the starting point for the study of the varieties deviating from it in one way or the other, we may turn first to the only form in the present material whose whorls are decidedly thicker than those of the *forma typica*. In the fragment U.S.N.M. No. 103916, here designated holotype of this variety (pl. 14, figs. 1, 5, text figs. 6, 39), the intercostal width of the whorls almost equals their height. This variety, for which the name *crassa* is here proposed, is further distinguished by its massive ornamentation; the ribs, of which there are at a comparatively early stage only four per quarter whorl, are strong and high, as are the nodes of all three rows and the denticulations of the keel.

[1] I am indebted to Dr. J. B. Reeside, Jr., for his communication (in a letter, dated Washington, July 21, 1943) that "the cross section, pl. 6, fig. 2, and the suture and lateral view, pl. 7, figs. 1g and 1h, are from the same specimen." According to Dr. Reeside, this specimen and those shown in figures 1e, 1f, and 3 of the same plate are only erroneously omitted among Meek's types, as listed in the type catalogue of the United States National Museum (1905, p. 535); the originals of figures 1e and 3, however, are indirectly listed there, viz., among the types of Stanton who refigured them in figures 4 and 3 of his plate 42 (1893).

[2] Reproduced as an index fossil by Grabau and Shimer, 1910, figure 1509c, as well as by Schuchert and Dunbar, 1941, plate 16, figure 2.

This is one of the rarest of the varieties of *P. woollgari;* in addition to the holotype just mentioned, only one specimen from the Carlile shale of north central Kansas (U.N. S.M. No. 1-12-12-37), attaining a diameter of about 320 mm., is, owing to its stout whorls and strong sculpture, with certainty referred to it. Besides, a scanty fragment from near Newcastle, Wyoming (U.S.N.M. No. 103908), exhibits the sculptural characters of this variety, without, however, having thicker whorls than the typical form, and may thus be considered transitional between both. A small nucleus associated with the aforementioned mold of a typical *P. woollgari* from the glacial drift of Iowa (U.S.N.M. No. 9083) is perhaps also referable to this variety whose development seems to be accelerated, as compared to the typical form.

It might be added here that Anderson's (1902, p. 125, pl. 1, figs. 11–16, pl. 10, fig. 202) *P. branneri* from the vicinity of Phoenix, Oregon, also differs from the typical *P. woollgari* Meek chiefly by being more inflated; being, however, much more densely and less sharply ribbed, it cannot be thought to include the new variety here established. The extreme variability of *P. woollgari* Meek, as shown in the present paper, suggests relegation of Anderson's form also to the rank of a mere variety (or subspecies?) of Meek's species.

(C) Var. **intermedia,** new variety

Plate 14, figures 2–4, 6–10, 12–16, plate 15, figures 1–6, 9, 10; text figures 7–9, 40–44, 46–58

Numerous specimens from the block from southern Utah and from various localities of the Black Hills area (U.S.N.M. Nos. 103896, 103902, 103909, 103911; A.M.N.H. No. 9529/2; S.D.S.S.M. Nos. 1315, 1672) are referred to this variety, as are Meek's specimens depicted in figure 1c, d, and 1f of his plate 7.

A comparison of his figure 1c and 1f does not leave any doubt but that both specimens belong to the same group within *P. woollgari,* whereas one of figure 1c, d, with figure 1a, b, discloses remarkable differences between the illustrated specimens. At a diameter of 30 mm. the ribs are much coarser and much farther distant from each other in the larger specimen, selected above as the lectotype of the typical form, than in the smaller one (per half whorl 8 in fig. 1a, as compared to 12 in fig. 1c). The latter, despite its historical priority and its good preservation, was not designated as the holotype of this variety, since it is exceptionally thin. An excellently preserved shell from the Black Hills (S.D. S.S.M. No. 1315, pl. 14, figs. 14, 15) is chosen for holotype instead. In addition, there are several good paratypes from various localities of South Dakota and Wyoming, two of which (U.S.N.M. Nos. 103909e and 103911) reach diameters of 65 mm., and some more from southern Utah (U.S.N.M. No. 103896). Another paratype from near Hot Springs, South Dakota (S.D.S.S.M. No. 1672b, pl. 15, figs. 1, 2), with excellently preserved suture lines (fig. 53), is remarkable for being markedly thicker than the holotype. The fragment described and figured by Johnson (1903, p. 141, pl. 12, fig. 31) from the Cerrillos Hills, New Mexico (Col. Univ. No. 15002), is tentatively referred to this variety.

The variety *intermedia* is more involute than the typical form, but less so than the variety *regularis;* also the costation remains dense and comparatively fine up to a later stage than in the *forma typica,* but the ribs begin earlier to be set farther apart than in the variety *regularis,* and fine secondary ribs are sometimes intercalated between the primary ones. The external nodes develop later and to a lesser degree than in the typical form and become elongated spirally to almost the same extent as in the latter, only at a comparatively late stage. On the other hand, these external nodes appear earlier and are altogether clumsier than in the variety *regularis.* In average thickness this variety about equals the *forma typica* but distinctly exceeds the variety *regularis.* The intermediate position between the typical form and the variety *regularis* which the present variety occupies has been alluded to in its name.

(D) Var. **regularis,** new variety

Plate 16, figures 1–17; text figures 10–12, 59–74, 78, 80, 81, 83

The largest and best-preserved full disk of this variety (S.D.S.S.M. No. 1470, pl. 16, figs. 14, 16, text figs. 80, 81) has been selected as its holotype. In addition, there are numer-

ous good paratypes from the Black Hills area and from the block from southern Utah (U.S.N.M. Nos. 103897, 103903, 103910, 103915; S.D.S.S.M. Nos. 1074, 1673).

Among all the forms of *P. woollgari* examined, this variety is the most involute (see, e.g., the holotype, pl. 16, fig. 16, and the paratype U.S.N.M. No. 103897a, pl. 16, fig. 5). It is, as a rule, slightly thinner than both the typical form and the variety *intermedia* and is distinguished by flat sides and marked lateroventral edges and, above all, by keeping its dense and very regular ornamentation, with uniform, more or less straight ribs and equally uniform outer nodes and denticulations of the keel, up to a comparatively large size. Both outer tubercles and teeth of the cockscomb-like keel, each of them corresponding to one pair of ribs, become slightly elongated spirally only at a very late ontogenetic stage, in contradistinction to the typical form and the varieties *crassa* and *intermedia*.

(E) Var. **tenuicostata**, new variety

Plate 16, figures 18–21; text figures 13, 14, 75–77, 82

This is a rare form; in addition to an almost full disk from the vicinity of Newcastle, Wyoming (U.S.N.M. No. 103904, pl. 16, figs. 18–20; text figs. 13, 14, 82), attaining only about 27 mm. in diameter and here selected as the holotype of this variety, about 20 fragments from the block from southern Utah are referable to it.

It is more involute than the typical form and the varieties *crassa* and *intermedia*, but less so than the variety *regularis*. Most characteristic of the present variety is its ornamentation. Up to a diameter of about 20 mm. it is extremely dense and fine, consisting of decidedly sigmoidal ribs; later they become, rather suddenly, much more distant from each other and markedly stiffer, almost straight. Both outer nodes and denticulations of the keel appear rather late (between the diameters of 15 and 20 mm.) and, where present, are only minute. Altogether this variety, whose earlier growth stages present a decidedly harpoceratoid aspect[1] (see pl. 16, figs. 19, 20), is somewhat stunted in its ornamentation and may represent a dwarfed form of the species under discussion.

[1] Already Hall and Meek (1854, p. 396) mention the "close resemblance [of their *Ammonites percarinatus*] to *A. aalensis* Ziet."

(F) Var. **praecox**, new variety

Plate 16, figures 22–33, plate 17, figures 1–5, plate 18, figures 1, 8, 9; text figures 15–18, 79, 84–90

This variety is not uncommon in two localities (designated Nos. 12642 and 18872 by the United States Geological Survey) of the Black Hills of South Dakota, where it is found to be associated with small specimens of *Holcoscaphites warreni* (Meek and Hayden) and with various pelecypods, but it is, within the material examined, not represented at any other locality of the Black Hills area or in the block from southern Utah. A medium-sized full disk from locality 18872 (U.S.N.M. No. 103913; pl. 17, figs. 1, 2, text figs. 88–90) is here designated holotype. Among the paratypes from the same locality, one (U.S.N.M. No. 103913e, pl. 17, figs. 3–5, text figs. 16, 87) is remarkable for attaining a diameter of about 125 mm., three more (U.S.N.M. Nos. 103913a, b, g; text figs. 17, 18; pl. 16, figs. 29, 32, 26, 27) for exhibiting early or even earliest growth stages. The specimen from Osborne County, Kansas, shown in Logan's (1899, pl. 24) figure 1, is believed to belong to this variety.

The variety *praecox* appears, at any stage, to deviate considerably from the typical *P. woollgari* and is also well distinct from all the other varieties of this species. Most distinctive is its ornamentation which is, however, subject to changes even more abrupt than in other forms of *P. woollgari*. In early youth it shows an elegant and regular, somewhat harpoceratoid aspect, but soon some ribs begin to stand out more prominently than the others, particularly around the umbilicus, and to carry stronger external tubercles. In the medium stage the secondary ribs gradually vanish on the flanks and withdraw to the venter, but later on they fade even there. In this stage the remaining costae become quite straight on the sides, whereas they are distinctly orad-concave in the typical form. Also the two outer nodes are not so clearly separated from each other as in the *forma typica*, nor are they ever elongated spirally to such an extent, or so

sharp as in the latter. Those on the latero-ventral edge develop into horns, whereas those of the outermost row gradually disappear at a comparatively early stage. Simultaneously the ribs become obtuse, the small inner tubercles, which have meanwhile developed from the raised innermost portions of the principal ribs, are shifted ventrad as far as the first third of the flanks, and the serration of the keel gradually flattens out so as to become almost imperceptible in the largest paratype (U.S.N.M. No. 103913e) at a diameter of about 100 mm. All these changes, recorded in Meek's original description for the growth stage between 4 and 7 inches, occur considerably earlier in this variety; this fact suggests, at least for its later ontogenetic phases, an accelerated development, as compared with that of the typical form. To judge by specimens in the present material that are undoubtedly referable to the *forma typica*, the above statement would hold true even if Meek's description of the seven-inch stage should be taken, as it seems to be, from the specimen depicted in figure 1g, h, of his plate 7 and figure 2 of his plate 6 (cf. p. 153, footnote 1), here designated the holotype of the variety *alata*. There is certainly some resemblance between the latter variety and the one here dealt with, for example in that, in both, the ribs can be followed ventrad up the horn. However, the variety *alata* can, at the same diameter, readily be distinguished by the greater prominence of its ribs and by its wing-like horns which cause the costal section to be inverse-trapezoidal, whereas it appears to be more or less rectangular in the variety *praecox*, if the comparatively small horns are left out of account. The accelerated development of this variety from maturity to the latest ontogenetic stages has been alluded to in its name.

The differentiation between stronger and weaker ribs and the later disappearance of those of the latter kind cause this variety, of all the various forms of *P. woollgari*, most to resemble the genus *Prionocyclus*. Furthermore, it is the only form of, or close to, *P. woollgari* here dealt with that might perhaps be granted the status of an independent species.[1] However, it resembles, in various growth stages, so closely other forms within the wide range here allotted to this species that it is, in my opinion, better considered merely a variety of *P. woollgari*.

(G) Var. **alata**, new name

Plate 18, figures 2, 7, 9; text figures 19–22, 91

This is another rare variety of *P. woollgari*, based on the specimen depicted in Meek's (1876) figure 1g, h on plate 7 and figure 2 on plate 6 as its holotype. Within the present material only a quarter whorl, corresponding to a diameter of about 125 mm. and septate throughout, and a single horn from a larger specimen, both from 2 miles southeast of Fairburn, South Dakota (U.S.N.M. Nos. 103912a, b), are referred to this variety. A single horn from another Black Hills locality of South Dakota (U.S.N.M. No. 103905) might also belong to it. A fragment of another single horn, found in the block from southern Utah attached to the specimen U.S.N.M. No. 103897k, might be referable to this variety as well as to the *forma typica* (cf. p. 153).

This variety is almost fully evolute; it is distinguished by the wing-like development of the outer portions of its ribs, clearly pointed out in Meek's original description and producing the whorl section shown in figure 2 of his plate 6, which is distinctly different from that found in shells of the same or even a larger size, but referred to the *forma typica* or to the variety *crassa* (see figs. 19–22 and Meek's drawing just quoted).

For comparison with the variety *praecox* reference is made to the preceding discussion of the latter.

[1] As considered, though merely for sutural reasons, by Logan (1899, p. 211).

ONTOGENY[1]

DIMENSIONS

In the following tables, D indicates the greatest diameter that could be measured, H the height of the last whorl from the umbilical seam to the periphery, H′ its height from the dorsum to the periphery, W the width of the intercostal (internodal) section, W′ that of the costal (nodal) one, U the width of the umbilicus. In measuring D, H, and H′, the height of the keel or of external tubercles ("horns") rising above the level of the venter has been left out of account. D is always expressed in millimeters and tenths thereof; the other dimensions are, unless otherwise noted, expressed in per cent of D or, if that proved to be impossible, of a smaller diameter which is in such cases explicitly indicated. In these percentage figures decimals have been reduced or increased, respectively, to full or half per cent.

[1] In the course of the preparation of the block from southern Utah (p. 151) a minute, almost spherical bead (U.S.N.M. No. 103901) was found which measures about 0.4 mm. in diameter and which might be the protoconch of an ammonite. It consists of dark, almost glassy shale with tiny speckles of light substance which might be remainders of the shell. There seem to be indications of an umbilicus and of spiral involution, but both these observations may be deceptive. Indefinite lines on the surface might be taken for, but are certainly not, septal margins, as no septa show in the interior of this bead in transmitted light. Since there is no certain evidence that this protoconch, should it be one at all, belongs to *P. woollgari*, it has not been included in the discussion of the ontogeny of this species.

Specimen No.	D	H	H′	W	W′	U
		(A) *Forma typica*				
U.S.N.M. 103895g	23.0 mm.	32	29	22½[a]	28½[a]	45
U.S.N.M. 103895d	26.1	35	33	?	?	44½
U.S.N.M. 103895b	28.2	29	24	23½	31	47
U.S.N.M. 103895c	31.2	32	28	?	?	45½
U.S.N.M. 103895a	32.4	32½	29	22[b]	29½[b]	44
U.S.N.M. 103895e	35.9	32½[c]	31[c]	27½[c]	34[c]	40[c]
U.S.N.M. 103895f	36.0	32	30½	20	33	45
U.S.N.M. 223[d] (lectotype)	67.2	35	?	30	35	42½
A.M.N.H. 25986:3[e]	*ca.* 317	34½	?	?	?	39
A.M.N.H. 25986:1[e]	*ca.* 356	33½	?	?	?	37½
		(B) Var. *crassa*				
U.N.S.M. 1-12-12-37	320.0 mm.	36[f]	?	33½[f]	*ca.* 48[f]	39[f]
		(C) Var. *intermedia*				
A.M.N.H. 9529/2:2	16.7 mm.	34½	*ca.* 30½	?	?	40
U.S.N.M. 103902a	23.2	35½	?	23½	25?	37½
A.M.N.H. 9529/2:3	23.3	35	31½	26	28	38½
U.S.N.M. 103896a	24.0	36½	32½	28	30	38
A.M.N.H. 9529/2:4	*ca.* 25	35[g]	30½[g]	25½[g]	29½[g]	38½[g]
U.S.N.M. 103902b	25.0	29½	?	?[h]	?[h]	38½

[a] Measured at D = 19.5 mm.
[b] Measured at D = 29.1 mm.
[c] Measured at D = 32.5 mm.
[d] Measurements from Meek's (1876, pl. 7) figure 1a, b.
[e] Specimens crushed.
[f] Measured at the greatest diameter unaffected by crushing, i.e., 215 mm.
[g] Measured at D = 21.3 mm.
[h] Specimen crushed.

Specimen No.	D	H	H′	W	W′	U
		(C) Var. *intermedia* (*continued*)				
U.S.N.M. 103896b	25.2	33	?	22½	28½	41½
U.S.N.M. 103944[a]	26.3	34½	?	?	?	35½
U.S.N.M. 103902c	27.2	38	?	29	30	37½
U.S.N.M. 103896c	27.5	32½	27½	?	?	40½
U.S.N.M. 103909a	27.7	36	?	28	29½	35
U.S.N.M. 103896d	29.0	34	30½	20	27	41½
S.D.S.S.M. 1672a	29.7	36½	33½	28	33½	39½
A.M.N.H. 9529/2:5	31.0	35	?	27½	32½	37
U.S.N.M. 103896e	33.1	37½	?	25½	30	35½
U.S.N.M. 103896f	33.6	38½	?	29	32	35
U.S.N.M. 103896g	35.1	40	?	25	31½	36½
S.D.S.S.M. 1315 (holotype)	39.0	40	32½	29	35½	35
U.S.N.M. 103896h	*ca.* 40	38½[b]	?	24½[b]	30½[b]	37½[b]
U.S.N.M. 103944a[c]	40.4	34½	?	21	26	40
S.D.S.S.M. 1672b	41.2	42	?	33	37	34½
U.S.N.M. 103911	*ca.* 65	37	32	23½	31	36½
		(D) Var. *regularis*				
U.S.N.M. 103910a	16.5 mm.	39½	?	?	32	32
U.S.N.M. 103910b	17.3	38	?	?	30	36
U.S.N.M. 103910c	18.1	37½	?	?	28½	36½
U.S.N.M. 103910d	*ca.* 25	36½	?	27[d]	27½[d]	36½[d]
S.D.S.S.M. 1074a	27.7	39	?	27½	28	33
S.D.S.S.M. 1074b	29.3	40½	32½	?[e]	?[e]	31½
U.S.N.M. 103897a	30.1	42½	?	29½	32	28½
U.S.N.M. 103897b	31.2	42½	35½	26½	26½?	33½
U.S.N.M. 103897c	32.3	42	?	?	?	32
U.S.N.M. 103897d	33.9	38[f]	32	25	30½	38½[f]
U.S.N.M. 103903a	30.4	42	35	?	*ca.* 27	33
	42.2	38	?	?[g]	?[g]	36
S.D.S.S.M. 1673a	43.7	42	?	25½	28	30½
U.S.N.M. 103903b	29.0	38	?	26½	27½	32
	46.5	38½	?	?[g]	?[g]	35
S.D.S.S.M. 1470 (holotype)	64.6	40½	38	31½[h]	32½[h]	30½
		(C) or (D) Type specimens of "*Ammonites percarinatus*" Hall and Meek				
A.M.N.H. 9530/1						
Smaller specimen[i]	5.8 mm.	35	?	?	?	37
Larger specimen[j]	24.4	36½	?	?	?	38½

[a] Measurements from Meek's (1876, pl. 7) figure 1f.
[b] Measured at D=36.6 mm.
[c] Measurements from Meek's (1876, pl. 7) figure 1c, d.
[d] Measured at D=22.9 mm.
[e] Specimen crushed.
[f] Abnormal involution with distinct egression of spiral.
[g] Specimen crushed.
[h] Measured at D=47.7 mm.
[i] Original of Hall and Meek's (1855, pl. 4) figure 2a.
[j] Original of Hall and Meek's (1855, pl. 4) figure 2b.

Specimen No.	D	H	H′	W	W′	U
		(E) Var. *tenuicostata*				
U.S.N.M. 103904 (holotype)	26.5 mm.	38½	35	?[a]	29[b]	37
		(F) Var. *praecox*				
U.S.N.M. 103913a	5.1 mm.	41	35	?	37	23½
	12.0	39	33½	?	32½	34
U.S.N.M. 103913b	16.7	40½	34	?	30½	39½
U.S.N.M. 103913c	18.1	35½	27½	?	30	38
U.S.N.M. 103906a	23.2	37½	?	?	31½	38
U.S.N.M. 103913d	31.2	39	?	*ca.* 29	*ca.* 32	38½
U.S.N.M. 103913f	38.5	38	35½	?	31	35½
U.S.N.M. 103913 (holotype)	84.4	*ca.* 40½	*ca.* 37	33½	36½	33
U.S.N.M. 103906b	89.8	39½	?	*ca.* 26	*ca.* 32½	37
U.S.N.M. 103913e	*ca.* 125	37[c]	?	*ca.* 28[c]	*ca.* 32[c]	37[c]
		(G) Var. *alata*				
U.S.N.M. 103945[d] (holotype)	*ca.* 170 mm.	34	28	23½	49	40½

[a] Owing to the density of costation the intercostal width could not be measured.
[b] Measured at D = 19.5 mm.
[c] Measured at D = 107.9 mm.
[d] Measurements from Meek's (1876) plate 6, figure 2; plate 7, figure 1g.

The following deductions may be drawn from the above table:

1. The degree of involution is lowest in the typical form, highest in the variety *regularis*, the other varieties occupying various positions in between. In this respect the variety *praecox* appears to be closest to the variety *regularis*, whereas the varieties *crassa* and *alata* are fairly close to the *forma typica*. In the latter, U always considerably exceeds H as it does in the single specimens of the varieties *crassa* and *alata* that could be measured. In the variety *regularis*, on the other hand, U is, with only two exceptions, considerably smaller than H; the same relation prevails, as a rule, in the variety *praecox* also. H exceeds U, though only slightly, in the only measured specimen of the variety *tenuicostata*. The variety *intermedia* occupies an intermediate position in this respect as well as in others; up to a diameter of 31 mm., U exceeds H to a higher or lower degree or, quite exceptionally, equals it, whereas in specimens of a larger size H is, with a single exception (Meek, 1876, pl. 7, fig. 1c), greater than U.

2. Ontogenetically a certain increase of the degree of involution in the typical form might be inferred from the table of dimensions. This inference might, however, be deceptive, since the reference of the giant disks at the bottom of the first section of the table to the typical form is not altogether certain. Even if it were, it must be kept in mind that they are badly crushed and their proportions in consequence distorted, since by such flattening D and H are caused to appear greater and U is caused to appear smaller than they would in an uncrushed shell. Thus no deviation from the general observation in Mesozoic ammonites, that large, gerontic disks are usually more evolute than smaller ones, can reliably be inferred from those figures. Nor can any definite trend be recognized in the smaller individuals; it is true that the amount of U in the lectotype (42½) is smaller than in the others where it comes, as a rule, close to 45, but U is found to be only 40 in specimen U.S.N.M. No. 103895e, which measures only 32.5 mm. in diameter. In the variety *intermedia*, however, a slight increase in involution can be found as far as the measure-

ments go, viz., up to a diameter of about 65 mm. In the variety *regularis* the umbilicus seems to be, on an average, slightly narrower at a diameter of about 30 mm. than above and below this mark. No definite trend in this respect is recognizable in the variety *praecox*, if the high degree of involution of the innermost whorls, measured in specimen U.S.N.M. No. 103913a at a diameter of as little as 5 mm., is left out of account.

3. On the whole, the tables confirm that the thickness is highest in the variety *crassa*. The same, or almost the same, intercostal width is attained by a particularly thick individual (S.D.S.S.M. No. 1672b) of the variety *intermedia* and by the holotype of the variety *praecox*. The average thicknesses of the three commonest forms, viz., the typical one and the varieties *intermedia* and *regularis*, and the thickness of the holotype and only measured specimen of the variety *tenuicostata* are about the same. It must be emphasized that the above statements relate to the intercostal width of the whorls (W), the costal one (W′) depending, for the amount exceeding W, on the height of the ribs and nodes. The difference between both is particularly marked in the variety *crassa*, where it approaches 50 per cent, and, even much more so, in the variety *alata*. Owing to the extreme development of the wing-like horns W′ is more than twice W in Meek's specimen here designated the holotype of this variety and about 1.6×W in the fragment U.S.N.M. No. 103912a, corresponding to a diameter of about 125 mm. (as compared to the holotype's diameter of about 170 mm.). The ratio H : W′ amounts to 0.63 in this fragment and to 0.7 in the holotype.

These ratios cannot be measured in the giant specimens tentatively referred to the typical form because all are badly crushed. However, since the penultimate outer tubercle of the largest disk (A.M.N.H. No. 25986:1) stands at least 50 mm. high above the surface of the intercostals, the difference between W′ and W must have been quite considerable in these shells also.

4. Owing to the scarcity of medium-sized specimens the above tables exhibit a wide gap between the diameters of 67 and 317 mm. for the *forma typica*, and measurements above a diameter of 65 mm. are entirely missing for the varieties *intermedia* and *regularis*. Only the ratios W : H and W′ : H could approximately be measured in some fragmentary specimens of and above medium size. Two of them are of about the same diameter. In the one (U.S.N.M. No. 103907a, diameter about 140 mm.) referred to the typical form, W : H amounts to 0.84 and W′ : H to 1.10, in the other (Col. Univ. No. 15002, described and figured by Johnson, 1903, diameter about 150 mm.[1]), here tentatively referred to the variety *intermedia*, W : H amounts to 0.79 and W′ : H to 0.97. In Logan's fragment (C.N.H.M. No. 5932), here referred to the typical form, the ratio W : H reaches even 0.87.

ESTIMATE OF FULL SIZE

The overwhelming majority of the specimens examined and virtually all those prepared from the block from the Mancos shale of southern Utah are of small size, attaining only exceptionally, and hardly ever exceeding a diameter of 35 mm. Most of them are septate throughout, but some show the last septum at diameters between 20 and 35 mm., quite rarely at even smaller diameters. In the investigation of the sizes reached by the various forms of *P. woollgari*, as distinguished in this paper, these small individuals, which need not be adults, may well be left out of account. Rather has this investigation to depend on disks or fragments of diameters of 35 mm. and more (with the only exception the variety *tenuicostata*, none of whose specimens attains even 30 mm. in diameter). It is quite natural that very large shells, as the giant disks referred to the typical form on the one hand and to the variety *crassa* on the other, are rare, but also medium-sized ones or fragments thereof are scarce (see above, 4) and even diameters between 40 and 70 mm. are attained only by a few specimens within the material examined.

(A) Forma typica

Neither Meek's description nor his figures give any indication as to the beginning of the body chamber in the specimen shown in figure 1a, b, of his plate 7, here designated lectotype of the typical form, and the speci-

[1] Johnson's (1903, p. 141) estimate of 160 or 180 mm. is obviously too high.

men itself is inaccessible for examination under present conditions. In the medium-sized example U.S.N.M. No. 103907a the last septum can be located almost at the anterior end of the preserved part of the outer whorl, corresponding to a diameter of about 130 mm.; allowing from half a whorl to three-quarters for the body chamber, this conch may, when complete, have reached a diameter of 200 mm. or even more. Logan's aforementioned fragment (C.N.H.M. No. P5932), corresponding at its anterior end to a diameter of about 140 mm., is septate throughout; the disk to which it belonged must, therefore, have attained at least 250 mm. in diameter. Thus it seems really to have been "evidently much larger than any seen by Meek" (Logan, 1899, p. 213), since Meek (1876, p. 456) states the "largest specimen seen (with a part of the nonseptate portion wanting)" measured 7 inches (=178 mm.). As far as their size is concerned, the three giant disks (A.M.N.H. No. 25986) might thus well be referred to the typical form also; merely their poor preservation imposes some reserve as to their identification. The largest of these disks (A.M.N.H. No. 25986:1) is remarkable not only for its diameter of 356 mm., which makes it undoubtedly the biggest specimen of this species ever recorded, but also for exhibiting the apertural margin, observable in this shell alone among 445 examined, and thus allowing one to measure the size of the complete disk instead of merely estimating it. On the other hand, the beginning of the body chamber cannot be located in any of these disks. In one of them (A.M.N.H. No. 25986:2) suture elements can still be seen at a diameter of about 190 mm., and in the biggest one, just mentioned, at a diameter of about 140 mm., but in neither case do they seem to belong just to the last septum; hence the length of the body chamber cannot reliably be determined. In the largest disk present the apertural margin runs in a decidedly rursiradiate direction across the umbilical wall, then changes its direction on the umbilical shoulder and continues in an almost straight, slightly prorsiradiate line toward the periphery, thus forming an orad concave, rather shallow sinus on the inner half of the side (pl. 14, fig. 11). The growth striae, particularly well recognizable on and near the umbilical wall at the anterior end of the outer whorl, run parallel to the apertural margin. It is worth noting that the test, attaining a thickness of from 5 to 6 mm. on the penultimate outer horn, seems to become thin and delicate near the apertural margin.

(B) Var. crassa

In both the holotype (U.S.N.M. No. 103916) and the transitional specimen (U.S.N.M. No. 103908) the last septum is found at a diameter of about 60 mm., whereas the giant shell from north central Kansas (U.N.S.M. No. 1-12-12-37) is septate at least up to a diameter of 220 mm. Since the spiral continues for another half whorl up to a diameter of 320 mm., this conch cannot be far from complete. Anyway, this variety seems to have reached about the same considerable size as the typical form.

(C) Var. intermedia

The last septum cannot be located in the holotype which is almost entirely covered with the test; at least the anterior quarter of the outer whorl is unseptate, although this specimen attains only 39 mm. in diameter. However, the paratype S.D.S.S.M. No. 1672b, though slightly larger than the holotype, is septate throughout, as is specimen U.S.N.M. No. 103909e which attains even a diameter of 65 mm. In another paratype of about the same size (U.S.N.M. No. 103911), however, the last septum is found at a diameter of 45 mm., the preserved anterior half of the outer whorl belonging to the body chamber. The same holds true for Johnson's fragment of an outer whorl from the Cerrillos Mountains of New Mexico (Col. Univ. No. 15002) which attains a diameter of about 150 mm. (cf. p. 160, footnote 1). It is true that no giant shells of this variety are available as in the two preceding forms, but a "gerontic" specimen also described by Johnson (1903, p. 142) from the Cerrillos Mountains and inspected by the writer in the collections of Columbia University "must," according to that author, "have measured from 250 to 300 mm. in its greatest diameter." Therefore, should both Cerrillos specimens be referable to the variety *intermedia*,

it may be assumed not to have been far inferior in size to the typical form. If, on the other hand, those specimens are left out of account, the present material allows one safely to assume only a diameter of from 120 to 150 mm. for a complete disk of this variety.

(D) Var. **regularis**

In two paratypes from near Newcastle, Wyoming (U.S.N.M. Nos. 103903a, b), attaining diameters of 42 and 46.5 mm., respectively, the last septum is found between the diameters of 20 and 25 mm. and at a diameter of about 30 mm., respectively, the anterior half of the outer whorls belonging to the body chamber. In the specimen S.D.S.S.M. No. 1673a, of about the same size, the last septum is also found at a diameter of about 30 mm. The holotype, however, which is also the largest known specimen of this variety, is septate up to its anterior end which corresponds to a diameter of about 65 mm.; when complete, it may have attained between 110 and 130 mm. There is no evidence of a greater size reached by this variety.

(E) Var. **tenuicostata**

If a specimen from the unnumbered block from southern Utah (U.S.N.M. No. 103899) believed to be transitional between this variety and the preceding one is left out of consideration, the holotype (U.S.N.M. No. 103904) is the largest specimen present, although it attains only a diameter of 26.5 mm. Despite its smallness the anterior half of its outer whorl belongs to the body chamber which begins at a diameter of only 18 mm. On the strength of the material available this rare variety must therefore be considered the smallest one of this polytypic species.

(F) Var. **praecox**

Some of the smaller individuals show the last septum at diameters of about 30 mm. or even less. In the largest paratype but one (U.S.N.M. No. 103906b) it is found at a diameter of about 55 mm., leaving more than half of the outer whorl with the body chamber, and in the holotype (U.S.N.M. No. 103913) at a diameter of about 80 mm.; here only the foremost part of the outer whorl is unseptate. The largest paratype (U.S.N.M. No. 103913e) is, however, septate up to a diameter of 106 mm.; less than a quarter of its outer whorl belongs to the body chamber which, when complete, may have readily attained between 175 and 200 mm. in diameter. This is the size that can be assumed at our present knowledge to have been reached by this variety.

(G) Var. **alata**

From Meek's (1876) description and figures it can be seen that his specimen illustrated in plate 6, figure 2, and plate 7, figure lg, h, here designated the holotype of this variety, measures about 135 mm. in diameter at the last septum and about 170 mm. at the anterior end. Meek states it to be the "largest specimen [of *P. woollgari*] seen." The only fragment in the present material permitting of examination in this respect, U.S.N.M. No. 103912a, just shows the last septum at its anterior end, corresponding to a diameter of about 125 mm.; it may be assumed to have reached almost the same diameter of about 200 mm. as the holotype. Thus the known representatives of this variety, even when supplemented to their full size, are far exceeded by the giant disks referred to the typical form and to the variety *crassa*, but they are almost equaled in size by the preceding variety.

WHORL SECTION

One of the earliest cross sections that could be studied belongs to the minute whorl fragment in the lot A.M.N.H. No. 9529/2, corresponding to a diameter of about 2.5 mm. and exhibiting no ornamentation whatsoever. Since no later parts belonging to the same individual are known, this fragment cannot be assigned to any definite form within this species. The section seen at its posterior end (fig. 1) is round, almost circular, with the greatest width somewhat nearer to the dorsal than to the ventral end. Another specimen too small to be referred to any given form (U.S.N.M. No. 103900[1]b) exhibits at its

[1] Under this catalogue number have been united all the United States National Museum specimens of *P. woollgari* from the block from southern Utah too small to be assigned to any of the forms here distinguished within this species.

anterior end (diameter 6 mm.) an oval section with indications of lateroventral shoulders, a pronounced, though blunt median keel, and a moderately deep impressed zone (fig. 2). Its maximum width is at about the second fifth of the height.

FIGS. 1–4. Whorl sections of *Prionotropis woollgari* Meek (? *non* Mantell).

1, 2. Shells too small to be assigned to any given form within the species; 1, a whorl fragment from the lot A.M.N.H. No. 9529/2; 2, U.S.N.M. No. 103900b; both ×5.

3, 4. *Forma typica*, U.S.N.M. No. 103895h; 3, at diameter of disk of *ca.* 5 mm.; 4, at diameter of disk of *ca.* 7 mm.; both ×5.

(A) Forma typica

The earliest stage at which a whorl section could be studied in a specimen definitely referred to the typical form (U.S.N.M. No. 103895h) corresponds to a diameter of about 5 mm. (fig. 3). It is oval and has its maximum width at about the first third of its height. The keel is already present. Costal and intercostal sections run parallel to each other, the former being just slightly wider than the latter. The general shape of the intercostal section has not yet changed much in the next stage, studied at a diameter of about 7 mm. in the same specimen (fig. 4), but the costal (nodal) one already shows on its top three distinct, almost equally high prominences, corresponding to the keel and the two outermost tubercles. The umbilical shoulder is well rounded, the impressed zone gently curved and shallow. The intercostal section remains oval, with pronounced, though rounded umbilical shoulders and a shallow impressed zone, in the next stage also, which is well shown by specimens U.S.N.M. Nos. 103895m and 103895e at diameters of about 15 and 19 mm., respectively (pl. 13, figs. 13 and 10). The costal one, however, approaches more and more a rectangular shape, with slanted upper corners and a three-pronged topside. It shows seven rather sharp prominences around its circumference, which correspond to the umbilical, lateroventral, and outermost nodes on either side and to the undulating keel. There is a slight concavity to be seen on the ribs between the umbilical and lateroventral nodes, a deeper one, corresponding to the slanted upper corners of the rectangle, between the nodes of the two outer rows, and the deepest one on either side of the keel. Thus a peculiarly scalloped aspect of the costal section is brought about even at this comparatively early stage. This aspect persists through the later stages of growth, as seen in the posterior ends of the whorl fragments U.S.N.M. Nos. 103895i and 103895j, corresponding to diameters of about 27 and 35 mm., respectively (pl. 13, figs. 6 and 5), with the prominences indicating the tubercles becoming gradually sharper.

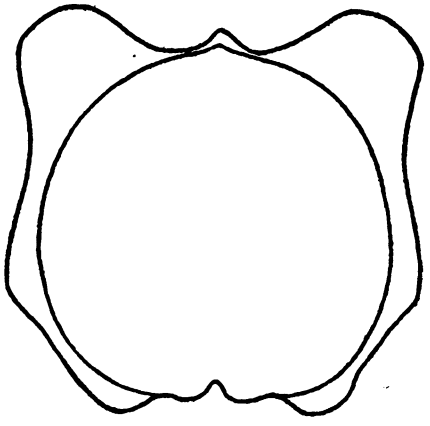


FIG. 5. Whorl section of *Prionotropis woollgari* Meek (? *non* Mantell), *forma typica*, C.N.H.M. No. P5932, natural size.

In the medium-sized example U.S.N.M. No. 103907a (pl. 13, fig. 7) the intercostal section at the posterior end of the preserved fragment of the outer whorl, corresponding to a diameter of not quite 100 mm., appears to be elliptic rather than oval, the greatest width being closer to the middle of the height, and the umbilical wall is steeper than in earlier ontogenetic stages. The surface of this whorl fragment is too much worn to allow a proper study of the costal section.

Both intercostal and costal sections can, however, be well studied in the whorl frag-

ment C.N.H.M. No. P5932 (fig. 5). In general outline the intercostal section is almost circular, the costal one almost quadratic, with deep concavities between the keel and the outer nodes, shallow depressions between the latter and the circumumbilical ones, and an umbilical wall sloping at an angle of about 60 degrees. The impressed zone amounts virtually to nothing.

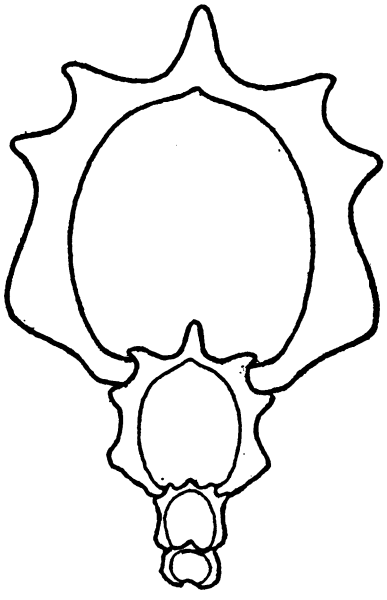


FIG. 6. Section across four consecutive whorls of *Prionotropis woollgari* Meek (? *non* Mantell), var. *crassa*, new variety; holotype, U.S.N.M. No. 103916; ×2.

The three giant disks tentatively referred to the typical form (A.M.N.H. No. 25986) are very badly crushed, and the sections observable at the fractures (now mended) of the last whorl of specimen No. 2 are, therefore, utterly distorted, the intercostal section being compressed to about one-seventh of its width. However, the costal section can still be recognized as exhibiting a considerable concavity on its sides, due to the prominence of both circumumbilical and outer tubercles.

(B) Var. crassa

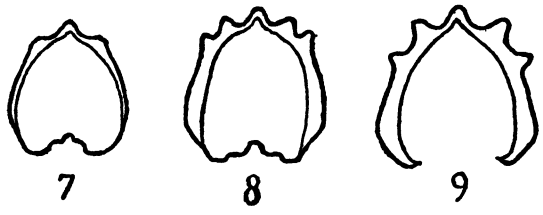
The cross section of this variety can be well studied in four consecutive whorls of the fragmentary holotype (U.S.N.M. No. 103916, fig. 6), corresponding to diameters of about 5, 15, 35, and 60 mm., respectively. The intercostal section is almost circular in the earliest of these volutions and broad-elliptical in the later ones; there is, except for the keel of the preceding whorl, hardly any impressed zone. Both umbilical and lateroventral shoulders are pronounced, though rounded. The umbilical wall is rather steep. The costal section resembles in general outlines that of the typical form, but it is considerably wider and both nodes and concavities are much more accentuated in the penultimate and even more so in the outer whorl, the section of the latter marking the scalloped character of this species at its peak (see also pl. 14, fig. 5). Most characteristic of this variety is the prominence of both the circumumbilical tubercles, which mark the maximum width of the costal section, and the teeth of the cockscomb keel, which considerably overtop the nodes of the two outer rows.

The section of the penultimate whorl of the paratype U.N.S.M. No. 1-12-12-37 up to a diameter of 90 mm. closely resembles that of the outer volution of the holotype. The anterior half of the outer whorl of the paratype is badly crushed. Its posterior half, however, reveals between the diameters of 125 and 200 mm. the section which here greatly differs from that seen in earlier growth stages. The intercostal section shows the outline of a quadrate with well-rounded corners and with the median keel rising to varying degrees above the topside. The umbilical wall slopes rather gently, and there is hardly any impressed zone. The costal section is characterized at this stage by the fact that the circumumbilical tubercles have withdrawn considerably ventrad to about the third eighth of the whorl height and that both the outer tubercles have amalgamated on either side into a strong, more or less blunt horn which far overtops the still undulating but low keel (pl. 15, fig. 7).

(C) Var. intermedia

The earliest whorl section studied in an individual definitely referred to this variety (U.S.N.M. No. 103896i, fig. 7) corresponds to a diameter of about 7 mm. and agrees fairly well with that described for the same stage in the typical form, except that here the outermost nodes are less developed and therefore more overtopped by the keel. At the posterior

end, corresponding to a diameter of about 12 mm., of another whorl fragment (U.S.N.M. No. 103896j) may be seen an oval, rather slender intercostal section and a costal one whose upper half is already distinctly scalloped (fig. 8). A somewhat wider and slightly more markedly scalloped section of another whorl fragment (U.S.N.M. No. 103896k) is shown for comparison in figure 9. Many changes in section do not seem to occur during the following growth stages. In some individuals, however, it becomes rectangular rather than oval, as seen by comparing the sectional view (pl. 14, fig. 4) of specimen U.S.N.M. No. 103896l, diameter about 25 mm., with that of the only slightly smaller specimen U.S.N.M. No. 103896m (pl. 14, fig. 2). Such flattening of the sides occurs more and more frequently at diameters above 30 mm., although in most of the specimens the sides are seen to converge ventrad more distinctly than in the aforementioned U.S.N.M. No. 103896l, e.g., in the fragment U.S.N.M. No. 103896n, whose anterior end, shown in plate 14, figure 3, corresponds to a diameter of about 30 mm. The same is also true of the holotype whose section is not illustrated separately; it can, however, be recognized in the ventral view of this shell (pl. 14, fig. 15) as being considerably scalloped. The same characters of the section as in the holotype are also found in the two biggest paratypes (U.S.N.M. Nos. 103909e, 103911, pl. 14, fig. 16) also, whereas the paratype S.D.S.S.M. No. 1672b (pl. 15, figs. 1, 2) deviates in section from the holotype not only by being thicker but also by having, at the same diameter of about 35 mm., blunter ribs on its sides. Johnson's (1903) large whorl fragment (Col. Univ. No. 15002), tentatively referred to this variety, resembles in section that of about the same size referred above to the typical form (U.S.N.M. No. 103907a), but it is somewhat less thick and its sides converge more decidedly ventrad. It may be added that the sections at both the anterior and posterior ends of the Cerrillos fragment are by no means so broad and almost depressed as they appear in Johnson's drawing (1903, pl. 12, fig. 31c).



FIGS. 7–9. Whorl sections of *Prionotropis woollgari* Meek (? *non* Mantell), var. *intermedia*, new variety; 7, paratype U.S.N.M. No. 103896i; 8, paratype U.S.N.M. No. 103896j; 9, paratype U.S.N.M. No. 103896k; all three × *ca.* 5.

(D) Var. **regularis**

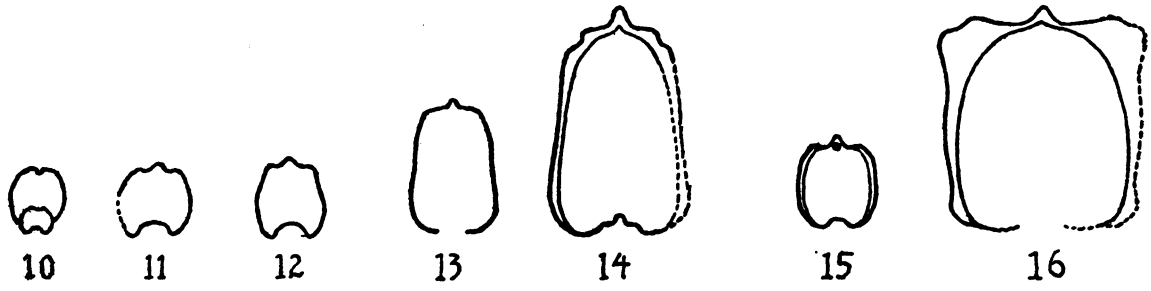
The innermost whorls of specimen U.S.N.M. No. 103897e broke out in the course of preparation so as to show their sections at diameters as small as 0.5, 1.3, *ca.* 2, and 3.2 mm. The earliest whorl section that could properly be studied in this specimen at a diameter of about 1 mm. (fig. 10) is considerably wider than high and gently rounded ventrally, without any trace of fastigation. At a diameter of about 2 mm. (same figure) the whorl is still wider than high, with the maximum width at about the first third of the height. There is still no fastigation of the venter; a distinct furrow indicates the site of the siphuncle instead. Soon, however, the venter begins to become fastigate, and at a diameter of about 3 mm. the first indication of a keel can be seen (fig. 11). This section is about as high as wide and subcircular in shape. In the same individual the section can further be studied at a diameter of not quite 6 mm. The intercostal section is oval, the costal one, with its sides already markedly flattened, approaches a rectangular shape. The impressed zone is less deep than in the earliest stages. The same oval to rectangular section can be recognized, at the diameter of 4.8 mm., in the nucleus of a small specimen (U.S.N.M. No. 103897f). Here the keel begins just to show in the sectional outline (fig. 12). In the next stage, best represented by specimen U.S.N.M. No. 103897g at a diameter of 14.3 mm., the nodes of all three rows also are visible in the costal section which slightly tapers ventrad and might, therefore, be called subtrapezoidal rather than rectangular. The intercostal section is oval, almost elliptical, the impressed zone only moderately deep (pl. 16,

fig. 4). With certain differences due to variation in whorl width, this type of section persists throughout the further development, as seen in the fracture of specimen U.S.N.M. No. 103903a exhibiting no fewer than four whorl sections, the last of them corresponding to a diameter of 29.2 mm. (pl. 16, fig. 11), and at the anterior end of specimen U.S.N.M. No. 103897d (diameter 33.9 mm., section, as shown in pl. 16, fig. 9, slightly dissymmetrical).

At the anterior end of the largest specimen studied, which is the holotype (S.D.S.S.M. No. 1470), the whorl section seems still to be about the same (diameter 64.6 mm.). This part of the shell unfortunately is damaged, but the ventral view (pl. 16, fig. 14) gives at least an idea of the costal section of this individual. Comparison with the ventral view of the considerably smaller holotype of the variety *intermedia* (pl. 14, fig. 15) and especially with that of the paratype U.S.N.M No. 103911 of that variety (pl. 14, fig. 16) well illustrates how much ornamental differences affect the costal section. Owing to the fact that the lateroventral nodes are just indicated in the variety *regularis*, but as strongly developed as those of the outermost row in the variety *intermedia* (and in the typical form and in the variety *crassa* as well), both sides and venter are markedly flat in the holotype of the variety *regularis*, and the outline of its costal section can hardly be called scalloped.

(E) Var. tenuicostata

The section of the holotype (U.S.N.M. No. 103904) seems to be oval, with pronounced lateroventral shoulders, and slender in the septate part of the conch where the ornamentation is so delicate that there is virtually no difference between costal and intercostal sections (fig. 13). In the body chamber the latter seems to be still oval, the former is slender and subtrapezoidal, with a hardly perceptible depression in the middle part of the ribs. The two rows of outer tubercles manifest themselves in sectional outline, and the keel is high and rather sharp (fig. 14). About the same section, though slightly distorted, is recognized at the anterior end of the fragment U.S.N.M. No. 103898a, corresponding to a diameter of 18.7 mm. (pl. 16, fig. 21). Another small fragment is remarkable for its comparatively deep impressed zone, indicating a higher degree of involution than in the holotype.



FIGS. 10–16. Whorl sections of *Prionotropis woollgari* Meek (? *non* Mantell).

10–12. Var. *regularis*, new variety; 10, 11, paratype U.S.N.M. No. 103897e; 12, paratype U.S.N.M. No. 103897f; all three ×5.

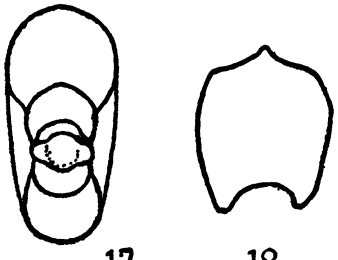
13, 14. Var. *tenuicostata*, new variety; holotype, U.S.N.M. No. 103904; both ×3.

15, 16. Var. *praecox*, new variety; 15, paratype U.S.N.M. No. 103906a, ×2; 16, largest paratype, U.S.N.M. No. 103913e, natural size.

(F) Var. praecox

Inner whorls of this variety could be exposed in specimens U.S.N.M. Nos. 103906c, 103913g, and 103913a at diameters between approximately 1 and 3 mm. An excellent natural cross section is visible in the last specimen (fig. 17). It exhibits the protoconch, which has the shape of a transversely elongated, somewhat spindle-like bubble, about 0.8 mm. wide and about half as high, the very depressed, slot-like aperture of the very

first whorl (diameter about 0.6 mm.), and two sections each of the second and third whorls (diameter 1.3 and 3.1 mm., respectively). Those of the second whorl are crescent-shaped and decidedly wider than high, those of the third are almost circular, if the impressed zone is left out of account. Its earlier section is still slightly wider than high; the later one, however, is already a little higher than wide; moreover, it is the first to show a slight indication of the keel. The section of the fourth whorl of this individual (diameter 5.2 mm., fig. 18) is subquadratic



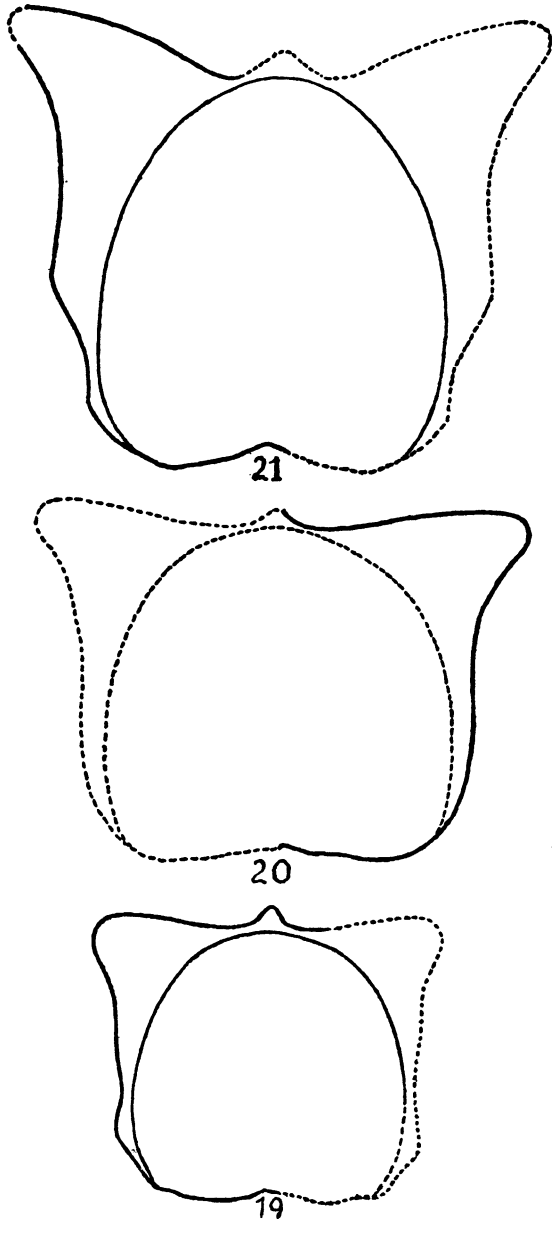
FIGS. 17, 18. *Prionotropis woollgari* Meek (? *non* Mantell), var. *praecox*, new variety; paratype U.S.N.M. No. 103913a; 17, section across the three innermost whorls, showing protoconch; 18, section of fourth whorl; both ×10.

in outline, somewhat higher than wide, with gently vaulted sides and well-rounded corners. On its topside the outermost nodes are just indicated, but the keel is quite pronounced even at this early stage. The impressed zone is rather shallow. The same fracture of this specimen includes another section half a volution later which corresponds to a diameter of about 8 mm. and shows still the same characters. The section shown by specimen U.S.N.M. No. 103906a at a diameter of about 13 mm. (fig. 15) differs from those just discussed merely by being slightly less wide and clearly elliptic. Very similar to the last section are those exhibited by specimens U.S.N.M. Nos. 103913b and 103913c at diameters of about 17 and 18 mm., respectively. The latter section (pl. 16, fig. 23) is the only one of this variety in which the sides converge ventrad. Otherwise this variety is remarkable for the more or less rectangular shape of its whorl section, well seen in the next stage, e.g., in the specimens U.S.N.M. Nos. 103906c (diameter about 23 mm., pl. 16, fig. 30) and 103913d (diameter 31.5 mm.). The costal section of the former individual is distinctly scalloped in its upper part.

Almost all the other small specimens present, or at least their body chambers, are crushed from a diameter of about 30 mm., so that sections cannot be studied. They can be, however, in the holotype (U.S.N.M. No. 103913) and in the largest paratype (U.S.N.M. No. 103913e) at diameters of from 50 to 125 mm. Two cross sections of the latter, corresponding to diameters of 70 and 102 mm., are shown in figure 16 and in plate 17, figure 3, respectively. In this stage the intercostal section is elliptic, the costal one rectangular; both external and umbilical shoulders are well rounded; the latter is particularly pronounced, and the umbilical wall is almost perpendicular. As seen best by comparing the ventral views of the holotype on the one hand (pl. 17, fig. 1) and of the biggest paratype on the other (pl. 17, fig. 5), the aspect of the costal section is intensely affected by the swift reduction, in this variety, of the sculpture on and near the venter (cf. pp. 179).

(G) Var. alata

The whorl section of the holotype of this variety has been illustrated by Meek (1876, pl. 6, fig. 2). His drawing seems to have been taken from the anterior end of this specimen which corresponds (*ibid.*, pl. 7, fig. 1g) to a diameter of about 170 mm. In the whorl fragment U.S.N.M. No. 103912a, the section can be well studied at diameters of about 100, 110, and 125 mm.; the sections seen at these diameters are shown in figures 19–21. Except for the last stage, even the intercostal section is wider than high and dome-shaped; the costal one is inverse-trapezoidal, with slight concavities along the ribs. From the tip of the horns the sectional outline slopes first gently, then, as growth progresses, more decidedly toward the median line, where it rises again, indicating the keel. The umbilical shoulder is pronounced, though rounded, the umbilical wall steep or even perpendicular. These sections differ from Meek's drawing chiefly in that the tips of the horns are only slightly less high than



FIGS. 19–21. *Prionotropis woollgari* Meek (? *non* Mantell), var. *alata*, new name; paratype U.S. N.M. No. 103912a; whorl sections at diameters of 100, 110, and 125 mm., respectively; all three natural size.

the keel, or equally high, or at the anterior end even markedly higher, whereas the keel far overtops the horns in Meek's figure. This seems, however, to be due to ontogenetic differences, the specimen here discussed being still septate throughout and smaller than the holotype, whose anterior part belongs to the body chamber. This view is supported by the second fragment from the same locality (U.S.N.M. No. 103912b) which represents a more advanced stage and in which the keel-like median line of the venter overtops the left horn (which alone is preserved) almost to the same extent as in the holotype (fig. 22). However, since the horn is much longer in the present fragment, the slope is considerably more gentle than in Meek's drawing.

ORNAMENTATION

Changes in the character of ornamentation, sometimes occurring rather abruptly, constitute the most striking ontogenetic features in the present species. The fact that they take place at different growth stages in the various forms distinguished within the species accounts, in particular, for the differences between the latter. This is true for the changes from dense and fine ribbing to a more widely spaced and coarser one, from sigmoidal costation to a stiffer one, for the appearance and the gradual vanishing of secondary ribs, for the appearance, development, and disappearance or amalgamation of the tubercles, and for the appearance of the keel and the development and final fading of its denticulations. In some cases a remarkable change in sculptural character coincides with the beginning of the body chamber, a phenomenon which might arouse some speculation. It must, however, be kept in mind that construction of septa goes on as long as the animal grows. Thus it cannot be argued that, as soon as it begins to build that part of the conch which is to be later its last living chamber, more calcareous substance becomes available for the outer shell than there was before. However, there seems to prevail a certain trend toward stronger construction of the definitive body chamber than of those parts of the conch which are only temporarily inhabited by the animal while it continues to grow.

Ornamentation sets in only at a somewhat advanced phase of life of the young animal, the innermost whorls being smooth. Insofar as this fact is observable in shells of which the later stages are preserved also, this smooth stage will have to be dealt with in the discus-

sion of the sculptural development of the respective forms. The material under examination includes, however, a few minute disks or fragments thereof which are much too small to be assigned to any of the forms here distinguished, but which deserve special attention and description for exhibiting the very first appearance of both keel and ornamentation. No indication of either is recognizable in the tiny whorl fragment from the lot A.M.N.H. No. 9529/2 which corresponds, at its anterior end, to a diameter of about 2.5 mm. and whose section has been described above (p. 162).

U.S.N.M. No. 103900b, whose whorl section also has been described above (p. 163), attains a slightly greater diameter (6 mm.) and seems to be a little thicker than the first. Here ornamentation begins somewhat later, at a diameter of 5.7 mm., and is restricted to folds on and near the lateroventral shoulder (zone of the future outer nodes); there are only three of them on about a sixth of a whorl. Fastigation of the periphery can here be recognized at a diameter of less than 3 mm. Then the venter is interrupted for about a quarter whorl and is preserved again only from a diameter of 5.6 mm., where

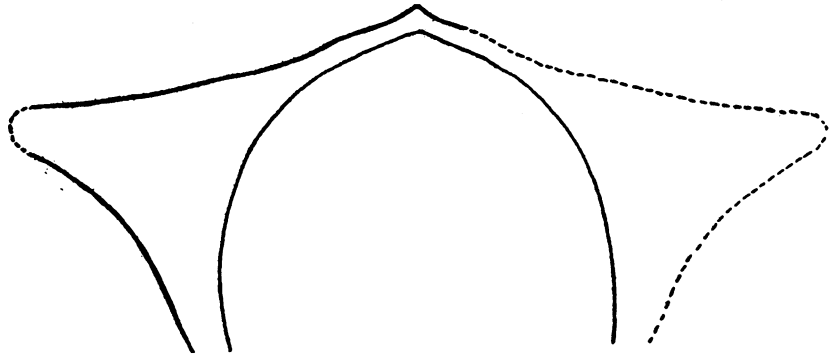


FIG. 22. *Prionotropis woollgari* Meek (? *non* Mantell), var. *alata*, new name; paratype U.S.N.M. No. 103912b; whorl section; natural size.

There are, furthermore, two very small but complete disks. One, U.S.N.M. No. 103900a, reaches a diameter of about 5 mm. and is unusually well preserved, so that from this diameter two whorls and a half can be followed in an apicad direction (pl. 13, figs. 2, 3). Ornamentation sets in at a diameter of about 4.5 mm. It consists of fold-like, slightly sigmoidal ribs which are distinct in the outer half of the sides only and show a slight swelling near the lateroventral shoulder (which might well be interpreted as foreshadowing the future outer tubercles). Every second of these ribs, five of which can be counted on a sixth of a whorl, seems to be slightly stronger than the preceding one. The ventral keel, heralded for about a quarter of a whorl by a fastigation of the periphery, becomes distinct at about the same spot where the costae first appear. Even at this early stage it shows a faint undulation, the peaks of these minute waves seemingly corresponding to the stronger ones among the ribs. The other disk, a distinct keel with very faint undulations is recognizable.

Two more minute disks (U.S.N.M. Nos. 103900c and 103900d), both attaining about 4 mm. in diameter, appear to be smooth up to a diameter of about 2 mm. At this size both show a shallow constriction; in the first individual there is another about a quarter whorl farther apicad. At the above diameter more or less distinct folds set in which are rather distant from each other and swell slightly at the first third of the sides so as to form faint tubercles (first indications of the circumumbilical ones?). Soon these folds are followed by ribs which gradually become more closely set. As many as 15 of them can be counted on the last quarter whorl of the first specimen, a surprisingly dense costation for this very early stage (between the diameters of 2.5 and 4 mm.). These ribs are almost straight and slightly prorsiradiate. Some can be recognized as starting at the umbilical shoulder and as standing out by being

stronger than the others, which are intercalated by two's and three's between them and begin only at some distance from the umbilicus. The ribbing of the second individual cannot equally well be studied; it is certainly less dense. No indication of a keel can be found in these two shells up to diameters of 2 and 2.5 mm., respectively; later on the peripheries cannot be examined.

(A) Forma typica

Among approximately 135 specimens referred with certainty to this form one only (U.S.N.M. No. 103895k) allows the observation of the first appearance of ornamentation. Here the external region of a half whorl is visible whose ends correspond to diameters of 1.7 and 2.9 mm., respectively. Its posterior half is still smooth, whereas the anterior one shows about six folds, which become more rib-like ventrad and markedly swell on the lateroventral shoulder, and the beginning of a blunt keel. Thus the first appearance of both keel and ribbing can be located, in this individual, at a diameter of somewhat above 2 mm., i.e., at a considerably earlier stage than in the two first of the five isolated little shells described above. This result agrees fairly well with the observation made in a complete disk (U.S.N.M. No. 103895l) attaining about 30 mm. in diameter on whose innermost whorls single folds, apparently far distant from each other, can be seen as early as at a diameter of 2.5 mm., and is further confirmed in a shell of about the same size (U.S.N.M. No. 103895m), whose inner whorls are still smooth at a diameter of about 1 mm., but exhibit quite a regular costation at about 2.5 mm. Between that diameter and that of 4 mm., 10 rather sharp, straight, slightly prorsiradiate ribs, apparently beginning on the umbilical shoulder, can be counted per quarter whorl; on the lateroventral shoulder they turn decidedly forward and are distinctly raised. The median line is clearly marked by a slightly undulating keel.

The next sculptural stage can be observed in the same shell between the diameters of 6 and 8.5 mm. There are nine rather sharp, single ribs on a quarter whorl. They run in a straight, or but very slightly sigmoidal, prorsiradiate line across the sides and turn sharply forward on the lateroventral shoulder, simultaneously forming a slight prominence marking this shoulder in the sectional outline. A second, much more pronounced prominence, separated by a shallow concavity from the first, rises at the outermost end of the ribs. Their peripheric ends run obliquely toward the keel, thus accentuating the forward turn mentioned above. It might be worth noting that the tubercles that they carry are elongated merely in that obliquely forward direction. When viewed frontally, these outermost portions of the ribs show a trapezoidal silhouette, with the longer and gentler slope toward the side and the shorter, somewhat steeper one toward the furrow separating them from the keel. The undulation of the latter is still gentle but quite distinct, each denticulation corresponding to an intercostal (pl. 13, figs. 11, 12) and just overtopping the neighboring outermost tubercles.

Although the specimen here dealt with (U.S.N.M. No. 103895m) is not one of the best preserved in the present material, it offers one the opportunity of following the sculptural development from the earliest stages, described above, up to a diameter of about 30 mm. At a diameter of about 12.5 mm. the character of ornamentation is still the same as in the phase just described, except for the fact that the tubercles of both outer rows begin to assume a bead-like shape. Then one of the most remarkable changes sets in; the ribs begin to stand farther apart. As a transitional stage—restricted, however, to half a whorl or less—secondary ribs appear between the primary ones. They begin, as a rule, only at some distance from the umbilical shoulder, are altogether weaker than the others, and carry no outer tubercles or only considerably reduced ones. In the anterior third of the specimen under examination, viz., between the diameters of 20 and 30 mm., these secondary ribs are further reduced to faint folds which run in the intercostals parallel to the primary ribs but vanish before reaching the periphery. If these almost thread-like secondary ribs, which do not occur regularly, are left out of account, the intercostals are now from two to two and a half times as wide as the costae, whereas they are only a little wider than the latter in the earlier stages. There are now only five (primary) ribs per quarter whorl. This condition

is, however, reached at various diameters in different individuals: e.g., in the characteristic specimen U.S.N.M. No. 103895h and, to judge by Meek's (1876, pl. 7) figure 1a, in the lectotype at about 20 mm., somewhat later than in the specimen just described.

Simultaneously another important change in ornamentation occurs even more abruptly. At a diameter of about 17.5 mm. the tubercles of both outer rows, which hitherto have kept in line with the general direction of the outermost portions of the ribs, begin to become elongated in a spiral sense, putting forth, as it were, spurs obliquely backward from the crest of the rib. These spurs develop at a surprising speed into ridges which, along with the cockscomb keel, soon dominate the ventral aspect of the shell. All four of these ridges converge apicad. They are, of course, not always equally distinctly developed; they may be said to be most pronounced and, at least locally, best preserved in specimen U.S.N.M. No. 103895h at a diameter of about 30 mm. (pl. 13, figs. 14, 15; see also the specimen immediately to the right of the label in pl. 11). Here they are strikingly sharp, much more so than in the lectotype whose ventral view (Meek, 1876, pl. 7, fig. 1b), it is true, represents a considerably later ontogenetic stage. On either side of the former individual both these ridges, which at this particular phase have replaced the outer tubercles, are highest at their anterior ends, where they join the steep anterior slope of the rib which is deeply notched between them. From this anterior end the ridge, which has developed from the outermost tubercle and which is in this individual sharp as a knife, runs backward, at first parallel to the keel, then turning toward it, and vanishes only at a short distance from the anterior slope of the preceding rib. The ridge that has developed from the lateroventral node is shorter than the former, but almost equally sharp. It is slightly curved and runs at an angle of about 45 degrees obliquely backward toward the median line, vanishing at the foot of the posterior slope of the rib.

At this stage the keel is still only gently serrated; each of its low denticulations corresponds to an intercostal. Their peaks are a little higher than the preceding outermost tubercles, accounting with them for the peculiar, three-pronged sectional aspect of the venter (pl. 13, figs. 14, 15), but just equal in height the following ones. It may be added that the sharp ridges which run from the peaks of the outermost tubercles obliquely forward toward the keel and end only at a short distance from it are nothing else than the external ends of the ribs. The latter are, in this stage, remarkably high and sharp, even before reaching the zone of the lateroventral tubercles. Here and there they are high and sharp at their inner ends also, thus suggesting circumumbilical tubercles. It might, however, be better to follow Meek's (1876, p. 455) example in merely saying that they "become a little more prominent and compressed at their inner extremities." In many individuals, including the lectotype, there are as a rule no more than four ribs per quarter whorl present in this stage.

As seen in the fragment U.S.N.M. No. 103895n (pl. 13, fig. 18), the keel sometimes already assumes a true cockscomb-like aspect at a diameter of about 30 mm. It may be noticed in this fragment, as well as in two others which, however, belong to much bigger disks (U.S.N.M. Nos. 103895o and 103895p, pl. 13, figs. 16 and 17), that the teeth of the cockscomb slope more steeply orad than apicad.

Above the diameter of 35 mm. the sequence of growth stages available for ontogenetic studies is much less complete than in the smaller sizes. How further changes in sculptural character, which are very considerable, come about can be construed piecemeal from Meek's drawings of the lectotype and from various specimens present. The first of these changes is well observable in Meek's (1876, pl. 7) figure 1a and in the artificial cast of a natural mold from the glacial drift of Black Hawk Creek, Iowa (U.S.N.M. No. 9083). The ribs become higher and sharper; simultaneously, the spiral elongation of the lateroventral tubercles is gradually lost and they become more or less conical, pointing strictly outward. The outermost tubercles, or ridges representing them, though still elongated and compressed in the spiral sense, become shorter, straight, and more or less parallel to the keel (Meek, 1876, pl. 7, fig. 1b). The next stage, at diameters between 100 and 125 mm., is represented chiefly by

the incomplete and worn cast U.S.N.M. No. 103907a (pl. 13, figs. 1, 7). There are still four ribs per quarter whorl. They are now altogether less sharp, but distinct. Radially elongated circumumbilical tubercles have developed which are, however, situated somewhat ventrad of the umbilical shoulder, at about the first fourth of the whorl height. The lateroventral tubercles—none of which is entirely preserved—seem to have assumed a horn shape and far outgrown the outermost ones which are more or less relegated to spiral ridges on the ventral slopes of these horns. They now resemble, and are almost aligned with, and only a little lower than, the teeth of the keel which is still distinctly cockscomb-like, as seen in another fragment of the same shell size (U.S.N.M. No. 103-907c).

Although Logan's whorl fragment C.M. N.H. No. P5932 represents an only somewhat later growth stage, it clearly illustrates the development of the sculpture beyond that reached in the shells just discussed (pl. 13, figs. 4, 19). This fragment, about a sixth of a whorl, carries three rather strong ribs. They are radial in general direction and slightly sinuous; the middle one seems to be even a little rursiradiate in its outer portion. In addition, there are faint secondary folds at the anterior thirds of both the intercostals present and even fainter ones at their posterior thirds. The latter become visible only near the lateroventral shoulder where they swell slightly. The primary ribs culminate at about the first third of the whorl height in radially elongated circumumbilical tubercles. Much more prominent, however, are the lateroventral ones which are blunt and horn-like, though also a little elongated radially. They point laterally in ventral view and obliquely upward in sectional view (fig. 5) and considerably overtop even the high points of the keel, which is still comparatively sharp and gently undulating. It shows main serrations which correspond to the primary ribs and, in addition, minor ones in between. The latter seem to correspond to the stronger ones of the aforementioned secondary folds. There is no trace left of the outermost tubercles.

This fragment reduces, though not considerably, the wide gap between the specimen U.S.N.M. No. 103907a, described above, and the three giant disks A.M.N.H. No. 25986. This gap is, however, bridged to a certain degree by the fact that the penultimate whorls of the latter agree in size and more or less in sculpture with the former specimen. Thus the big shells may be correlated with earlier ontogenetic stages of the typical form and at least tentatively be referred to it. The penultimate whorls of all three, attaining diameters of from 130 to 140 mm., exhibit seven or eight indistinct, strongly prorsiradiate ribs per half whorl. Most of these ribs carry strong circumumbilical tubercles at the first third or second fifth of the sides. In the posterior parts of these whorls these tubercles are elongated in the sense of the ribs, but they tend to become more and more conical later. Outer horns seem to be present, but neither they nor the periphery can anywhere properly be studied. The outer volutions carry 10 or 11 strong inner tubercles at about the same place as the penultimate ones. These tubercles are conical at first, but become again more and more elongated and compressed radially in the anterior half of the outer whorls, thus again indicating ribs. The latter become more distinct toward the anterior end, though as broad, blunt folds only (pl. 14, fig. 11). Now they follow a radial direction, connecting the inner tubercles with the even stronger outer horns. The latter are preserved only here and there and seem to be, as a rule, somewhat compressed in the spiral sense and to point upward and sidewise in sectional view. On the biggest disk (A.M.N.H. No. 25986:1), however, the penultimate outer tubercle rises as a strong, rather sharp spine almost perpendicularly about 60 mm. above the surface of the intercostal. As pointed out above (p. 161), the test that sheathed this horn[1] attained a thickness of about 6 mm. For description of the growth striae visible near the apertural margin, reference is made to page 161. No traces of the former outermost tubercles or of the keel could be found in any of these three disks which are, however, as may here be repeated, badly crushed.

In the preceding section the ornamentation

[1] This sheath mysteriously disappeared in the course of the preparation of this paper. Apparently it fell victim to a souvenir hunter.

of the typical form has quite intentionally been followed through its various ontogenetic stages in considerable detail to enable the writer to restrict the following sections to the description of those characters by which each of the single varieties of this polytypic species deviates in ornamentation from the corresponding growth stages of the typical form.

(B) Var. **crassa**

Only two specimens, widely differing in size but for this reason well supplementing each other, are available for a study of the sculptural ontogeny of this variety. One is the holotype (U.S.N.M. No. 103916) which can be studied at four different stages corresponding to diameters of about 5, 15, 35, and 60 mm., respectively (pl. 14, figs. 1, 5). In the two earliest of these four stages only the sides of the whorls are visible. On the innermost whorl preserved (diameter about 5 mm.) four closely set ribs can be counted on a sixth of a volution. They are farther apart on the next whorl (diameter about 15 mm.) where there are five per quarter whorl. Hence, it can be seen that the remarkable decrease in density of costation, observed in the typical form between the diameters of 15 and 20 mm., sets in considerably earlier in this variety. Already on this whorl the ribs are rather sharp and high, somewhat sigmoidal and prorsiradiate, and carry distinct circumumbilical tubercles at about the first third of the whorl height. Lateroventral tubercles are just visible at the contact with the umbilical wall of the following volution. In the latter (diameter about 35 mm.) the ribs have moved still farther apart, there being just four of them per quarter whorl. They have increased in strength and prominence. In addition to the circumumbilical and lateroventral tubercles, both of which are more pronounced and higher than in the preceding whorl, the outermost ones, too, can be seen in the anterior part of this volution. As in the *forma typica* at about the same size, these nodes are much elongated spirally. The lateroventral ones, however, are bead-shaped, and the circumumbilical ones are elongated radially. The keel is decidedly cockscomb-like. Its teeth considerably overtop the outermost tubercles. If allowance is made for the greater dimensions, the sculpture is essentially the same on the outer whorl (diameter about 60 mm.), part of which belongs to the body chamber, but the teeth of the keel are here higher still, and the lateroventral tubercles also show a trend toward spiral elongation. This individual may be said to exhibit most strikingly the peculiarities of ornamentation found in *P. woollgari*.

The other specimen that can be examined in this respect is the large paratype U.N.S.M. No. 1-12-12-37 (pl. 15, figs. 7, 8). Its reference to this variety is based not only on its great thickness, but also on the fact that it exhibits at the smallest diameter (about 80 mm.) at which the ornamentation can be studied the same sculptural features as the holotype at its anterior end. In the further course of growth, however, the character of the ornamentation changes repeatedly. Between the diameters of 100 and 130 mm. two or three secondary ribs are intercalated between two primary ones of which there are now only three per quarter whorl. The secondary ribs are much weaker than the primary ones and carry no circumumbilical tubercles and only indistinct lateroventral ones. Simultaneously the circumumbilical tubercles are shifted farther ventrad toward the middle of the sides which they reach in the next stage studied, between the diameters of 130 and 200 mm. There are no more than five primary ribs per half whorl, with a few indistinct folds between them, at this stage. They are marked by the inner tubercles and by much stronger, horn-like lateroventral ones. Most of the latter are somewhat elongated spirally and blunt at their tips. They point slightly obliquely backward in ventral view and sidewise and a little upward in sectional view, and slope steeply toward the sides, gently toward the median line. Hardly perceptible swellings on the outer slopes of one pair of these horns and some similar ones (perhaps belonging to obsolete secondary folds) in the intervals between the horns but corresponding in site to the former swellings are the only traces left of the outermost tubercles. The keel is broad and low and far overtopped by the horns in this stage, but still gently undulating, from two to three undulations corresponding to one pair of horns and the following interval. A grave

lesion of the conch occurred, perhaps in the animal's lifetime, at a diameter of 230 mm. and most seriously disturbed the sculpture of the shell between the diameters of 210 and 320 mm.; moreover, this part of the conch is much distorted by crushing. It can, however, be seen that the costation becomes denser again toward the anterior end, there being five primary ribs on the last quarter whorl, and that the inner tubercles, which were almost conical in the last stage discussed, become again much elongated radially. Altogether the sculptural character of this stage is similar enough to that of the three giant disks referred above to the typical form to warrant conspecificity. All that is left of the keel in the last ontogenetic stage is a faint median ridge, observable up to the middle of the last quarter whorl; preservation does not allow a decision as to whether or not it is entirely lost later. Distinct growth striation, running parallel to the ribs on the sides and in a slightly orad convex arch across the venter, is recognizable in the last part of this shell. It may be worth noting that all sculptural elements, costae and intercalated folds as well as growth striae, start at the umbilical wall and turn forward on the umbilical shoulder only.

(C) Var. **intermedia**

In thirteen individuals which can safely be referred to this variety (holotype and paratypes S.D.S.S.M. Nos. 1315, 1672a, and 1672b; U.S.N.M. Nos. 103909b, 103902d, 103896o, 103896p, and 103896q; A.M.N.H. Nos. 9529/2:1, 9529/2:2, 9529/2:3, 9529/2:4) the first appearance of folds can be observed at diameters between 1.5 mm. and almost 3 mm., but in a single specimen (A.M.N.H. No. 9529/2:5) they appear unusually late, at a diameter of 5 mm. only. Of all these shells only U.S.N.M. Nos. 103909b and 103896q and A.M.N.H. No. 9529/2:1 exhibit the periphery at a comparatively early stage. In all of them a distinct keel shows at a diameter of about 3.5 mm., but it is stronger and more distinctly serrated in the first specimen than in the other two.

Not only does ornamentation make its first appearance at different diameters in various individuals, but they differ widely in its development during the first sculptural stage, viz., up to a diameter of about 10 mm. For example, in the paratype S.D.S.S.M. No. 1672a (pl. 14, fig. 10) only indistinct folds, swelling to form blunt nodes at about the middle of the sides, can at first be seen. From a diameter of about 4 mm. these folds become more distinct in the outer half of the sides, but there are only three per quarter whorl. Only at a diameter of about 6 mm. do two or three secondary ribs begin to appear, first in the outer half of the sides, between the primary ones which up to a diameter of about 10 mm. stand out by being much stronger than the others. They can also be recognized at the same growth stage in the holotype (pl. 14, fig. 14); here differentiation between primary and secondary ribs becomes pronounced at a diameter of about 6 mm., chiefly owing to the development of strong umbilical tubercles in the former. Below that diameter a rather uniform and dense costation consisting of as many as 20 to 22 ribs per half whorl can be seen. The costation is equally dense and fine in specimens U.S.N.M. Nos. 103902d (pl. 14, fig. 8) and 103896h (pl. 15, fig. 5), but both deviate from the holotype by the lack of any differentiation between primary and secondary ribs in this stage. The same characters are found in most of the other individuals enumerated above, except for the paratype S.D.S.S.M. No. 1672b, whose sculptural peculiarities will be mentioned below. In the largest measured paratype (U.S.N.M. No. 103911, pl. 14, fig. 13) the ribbing between the diameters of 6 and 13 mm. is only a little less dense than in the holotype, but so weak as to be hardly perceptible.

The next sculptural stage, between the diameters of 10 and 20 mm., is characterized in the holotype by the fact that the costation becomes more uniform, there being but here and there a rib which starts at some distance from the umbilical shoulder but is otherwise hardly weaker than the others, and by the gradual development of the tubercles of the two outer rows. The circumumbilical tubercles have meanwhile almost disappeared. Only the outermost nodes begin to be elongated in a spiral sense. Simultaneously, the teeth of the keel have become prominent and sharp; they are now considerably higher than the outermost tubercles. In this variety also each corresponds in site to an intercostal, and

they slope more steeply orad than apicad. The holotype carries at this stage 15 ribs per half whorl. The above description holds equally true for the paratype S.D.S.S.M. No. 1672a and for the specimen depicted in Meek's (1876, pl. 7) figure 1c, d. All these individuals seem, however, to have reached maturity comparatively early. In others, e.g., U.S.N.M. Nos. 103896d and 103896h (pl. 14, fig. 6, and pl. 15, fig. 5) and 103909e, ornamentation develops more slowly. Fineness and density of the costation persist longer, as there are, between the diameters of 10 and 20 mm., as many as 20 to 23 ribs per half whorl, and both the outer tubercles and the serrations of the keel just begin to be more pronounced. The same sculptural characters are also seen in Meek's (1876, pl. 7) figure 1f. Development is even slower in the largest paratype measured (U.S.N.M. No. 103911, pl. 14, fig. 13). Here the costation remains very fine and dense (15 ribs per quarter whorl) up to the anterior end of the preserved part of the penultimate volution (diameter 27 mm.).

The next stage, approximately between the diameters of 20 and 35 mm., brings about the most important sculptural changes. The (primary) ribs begin to stand much farther apart, and the tubercles of the outermost row become elongated obliquely spirally. In this stage, too, a certain amount of variation is recognizable within this variety. In the holotype secondary ribs play a most subordinate part in the course of these changes. There is just one rib, at a diameter of not quite 30 mm., which is markedly weaker than the others on the sides but nonetheless carries outer tubercles, although they are somewhat reduced. The tooth of the keel that corresponds to these tubercles is also considerably lower than its neighbors. Later, only faint indications of secondary ribs can be found in two intercostals. There are 10 primary ribs on the last half whorls of the holotype, as well as of the paratype S.D.S.S.M. No. 1672a which resembles it closely, but shows more secondary ribs which are, moreover, not so much weaker than the primary ones as in the holotype. In some other individuals, e.g., U.S.N.M. Nos. 103896f and 103896g (pl. 15, figs. 9, 10), secondary ribs, sometimes even two of them between two primary ones, occur more regularly, and outer tubercles as well as denticulations of the keel are less developed than in the holotype. It may be added that sharp and high circumumbilical tubercles appear again toward the anterior end of the latter.

No more secondary ribs are found beyond the diameter of 30 mm. This stage of ornamentation is well illustrated by the preserved quarter of the outer whorl of specimen U.S.N.M. No. 103896h (pl. 15, fig. 5), which differs from the holotype chiefly by having less pronounced denticulations of the keel and slightly denser costation (six ribs per quarter whorl, as compared to five in the holotype). On the other hand, the last sculptural stage shown by this specimen connects well with the next, corresponding to diameters from 45 to 70 mm. and observable only in the two half disks U.S.N.M. Nos. 103911 (pl. 14, figs. 13, 16) and 103909e, whose outer whorls perfectly agree with each other. On the other hand, they closely resemble in both side and ventral views the lectotype of the typical *P. woollgari* (Meek, 1876, pl. 7, fig. 1a, b). They differ from it merely by having denser costation (about 10 ribs per half whorl, as compared to seven in that lectotype) and markedly lower teeth of the cockscomb keels.

The only individual within the material examined that allows the study of the ornamentation at an even later stage is that figured by Johnson (1903; Col. Univ. No. 15002). It is closely comparable to the specimen U.S.N.M. No. 103907a, referred to the typical form and described as to ornamentation above (p. 172). The former shell shows, however, denser costation (six primary ribs per quarter whorl, as compared to four in the latter), smaller lateroventral nodes, which have not yet absorbed the outermost ones to such a degree as in the United States National Museum specimen, and lower and less pronounced serrations of the keel. In addition, two secondary ribs are seen in Johnson's type. Some of these differences are the same as those found above to prevail between the lectotype of the *forma typica* and the specimens of the same size referred to the present variety. This fact may well support the proposed taxonomic assignment of the large individuals here discussed.

Finally, mention should be made of the distinctive characters found in the paratype S.D.S.S.M. No. 1672b (pl. 15, figs. 1, 2) which otherwise closely resembles the holotype of this variety. Apart from being considerably thicker, its ornamentation is somewhat coarser and less dense throughout development. Also the ribs in the last third of its outer whorl are blunter and somewhat stiffer than in the corresponding portion of the holotype. These undeniable sculptural differences are, however, believed to be due to individual variation only. The aberrant specimen under discussion is thus left with this variety, all the more so since its ventral aspect (pl. 15, fig. 1) is strikingly similar to that of the holotype (pl. 14, fig. 15).

(D) Var. **regularis**

In specimen U.S.N.M. No. 103897e, whose innermost whorls are accessible to study (see p. 165), indistinct folds, best visible in the inner zone of the sides, appear first at a diameter of about 2 mm. and become more distinct, rib-like, and more closely set at a diameter of about 3 mm., simultaneously with the first appearance of the keel. In various other individuals that could be examined in this respect (U.S.N.M. Nos. 103897a, 103897f, 103903a, 103910c, and 103910d, S.D.S.S.M. Nos. 1074a and 1074b) ornamentation appears at diameters between 1.8 and 2.5 mm. Only a small, exceptionally involute disk (S.D.S.S.M. No. 1673b) seems to remain smooth up to a diameter of 5.4 mm.

The aforementioned specimen, U.S.N.M. No. 103897e, may well serve for the further study of the sculptural development of this variety as well, since it is preserved up to a diameter of about 35 mm. (pl. 16, figs. 7, 15). Between the diameters of 4 and 8 mm. there is a dense and regular costation, with from eight to 10 ribs per quarter whorl. The costae are rather uniform in this shell, as they are in some others (e.g., U.S.N.M. No. 103897f). In other individuals, e.g., U.S.N.M. Nos. 103903a, 103903b, 103910c, every second or third rib stands out by being stronger around the umbilicus than the others and by tending to form elongated circumumbilical tubercles at which bifurcation occurs occasionally. In the outer zone of the sides these differences between primary and secondary ribs disappear. On the lateroventral shoulder the ribs turn decidedly forward. This point marks the site of the lateroventral tubercles, just indicated in this early stage, whereas the outermost ones are already quite distinct. They are slightly, if at all, overtopped by the teeth of the keel which correspond in both site and number to the intercostals. Distinctive of the ornamentation of this variety, even at this early phase, are the regularity and uniformity of all the sculptural elements on and near the venter. This character persists through the next phase, between the diameters of 8 and 15 mm. Now the lateroventral tubercles become pronounced also, so as almost to equal those of the outermost row in prominence and sharpness. Only occasionally the ribs, 10 or 11 of which can now be counted per quarter whorl, assume a slightly sigmoidal course. There is not much change in the ornamentation during the next stage, between the diameters of 15 and 30 mm. It is still distinguished by its great density, regularity, and uniformity which can be recognized best in ventral view (e.g., U.S.N.M. No. 103903a, pl. 16, fig. 10). Secondary ribs occur quite frequently in this stage, as seen, for example, in the side view of the holotype (pl. 16, fig. 16). They differ from the primary ones chiefly by being weaker in the inner zone of the sides and by lacking circumumbilical tubercles, which are sometimes (U.S.N.M. Nos. 103897e and 103897i, pl. 16, figs. 15 and 3) markedly developed on the primary ribs. There are now 11 or 12 ribs per quarter whorl. The same density as in the costation is found in the serration of the keel; there are many fine teeth, separated by equally regular indentations. Neither these teeth nor the tubercles of the two outer rows are prominent in this stage. It is the costation rather that dominates the sculpture, and there is no scalloped aspect whatsoever. It is worth noting that in this variety, owing to the sharpness and regularity of the outermost tubercles, the ventral edges become particularly pronounced. Thus the periphery becomes truncate, gently sloping from the keel toward those edges.

In the last stage observable in the paratype U.S.N.M. No. 103897a (pl. 16, figs. 5, 6), when its diameter approaches 30 mm.,

the outer tubercles become less elongated radially, rather bead-shaped, and better visible in side view. The same holds true for a fragment of a somewhat larger disk (U.S. N.M. No. 103897h, pl. 16, figs. 8, 13). Here the outermost tubercles tend to become elongated spirally and are much more prominent than the lateroventral ones. This state of affairs is strongly reminiscent of that found in the paratype U.S.N.M. No. 103896h of the variety *intermedia* (pl. 15, figs. 4, 5), except for the greater density and fineness of the ornamentation of the fragment here discussed.

The further sculptural development seems, as in the preceding variety, to depend solely on the stage of growth at which maturity is reached, as indicated as a rule by the last septum. In the paratypes U.S.N.M. Nos. 103903a and 103903b, it is found at diameters between 20 and 25 mm. and of 30 mm., respectively. In both these individuals a rather sudden change in the character of ornamentation occurs at a diameter of about 35 mm. (pl. 16, figs. 12 and 17). The intercostals become much wider, and the ribs much coarser. Less than a quarter of a whorl later a sculptural character is reached which does not differ so much from that found in the mature stages of the variety *intermedia*. There are only five or six strong ribs per quarter whorl, with but occasional faint indications of folds intercalated between them, with sharp, more or less spirally elongated outer nodes, and radially elongated circumumbilical ones. The keel is deeply scalloped and decidedly cockscomb-like. In the holotype, on the other hand, which is septate throughout, the ribs step, from a diameter of about 40 mm., quite gradually farther apart and become blunter. Eight of them can still be counted along the periphery of the last quarter whorl (pl. 16, fig. 16). Simultaneously, the lateroventral nodes assume the shape of blunt, more or less circular knobs, whereas those of the outermost row become sharp, prominent, and spirally elongated. They are still closely set, thus accentuating the edges bounding the venter. From these edges the nodes continue, hardly tapering and sloping only gently, toward the keel which overtops them quite considerably. Its teeth, too, have become prominent by now, but they are still rather closely set, separated by interstices of about the same length. They exhibit, in side view, an almost regular triangular outline, without any considerable difference in slope between their apicad and orad sides. They still correspond in site and number to the intercostals. Some, which seem to be coordinated with secondary ribs, are inferior to their neighbors in both height and length.

(E) Var. **tenuicostata**

Except for the holotype and the mold of another disk of about the same size (U.S. N.M. No. 103917), this variety is represented merely by whorl fragments. Its sculptural ontogeny can best, and almost exclusively, be studied in the holotype (pl. 16, figs. 18–20). It is smooth up to a diameter of about 2 mm.; then indistinct folds appear which seem to swell slightly in the inner zone of the sides. Soon, however, the extremely fine and dense costation sets in which persists up to a diameter of 18 mm. Counting back from this diameter, there are as many as 70 elegant, slightly sigmoidal ribs per whorl which start at various distances from the umbilical seam and often bifurcate on the umbilical shoulder, but are otherwise quite uniform. The ornamentation on and near the venter can be studied from a diameter of 11 mm. only. The outermost nodes are just slightly indicated, but there is hardly any indication of lateroventral ones. The keel is comparatively strong but low, and undulates only gently, there being apparently only one indistinct denticulation to two or three ribs.

The character of the ornamentation changes rather abruptly at the beginning of the body chamber. On the anterior quarter of the outer whorl there are only eight rather stiff and comparatively strong ribs, separated by intercostals about twice as wide. In one a secondary rib can be seen which is in turn accompanied by a thread-like "tertiary" one. In their outermost section the costae carry distinct, though weak lateroventral and outermost nodes, the latter being better developed than the former and slightly elongated in the spiral sense. The keel is now rather sharp and distinctly serrated, every tooth corresponding in site and length to an intercostal. These teeth considerably overtop the outermost tubercles.

(F) Var. **praecox**

The sculptural development of this variety is characterized by even more frequent and more abrupt changes than that of any other form referred to this polytypic species. Here, too, the shell is smooth in the earliest stages, e.g., up to a diameter of 2.5 mm. in specimen U.S.N.M. No. 103913a, in which the innermost whorls could be exposed, as they could in U.S.N.M. No. 103913g. In the examples U.S.N.M. Nos. 103913d and 103913g the first folds can be observed at diameters of less than 1.5 mm. and 1.8 mm., respectively. In both, a dense, regular costation sets in immediately afterwards at diameters of about 2.5 mm., as compared to about 3.5 mm. in specimen U.S.N.M. No. 103913a, mentioned above. Up to a diameter of 6 or 7 mm., the costae, 18 of which can be counted per half whorl, remain uniform, then differentiation sets in. Three of four ribs per quarter whorl begin to stand out by being higher and stronger than the others, one, two, or exceptionally three of which are intercalated between two of them. This differentiation appears, however, earlier and is more distinct in some individuals than in others. in appears that the ribs are almost straight in the first group, but slightly sigmoidal in the second, represented best by U.S.N.M. No. 103906a (pl. 16, fig. 24). It is on the primary ribs that both circumumbilical and outer nodes develop in the next stage, between the diameters of 6 and 25 mm. In this stage all of them are elongated in the costal sense. The nodes of the two outer rows are amalgamated at first, then the outermost ones begin to become independent as slight transverse ridges across the ribs. The latter continue, gradually tapering, obliquely forward to the base of the keel. The keel, still fine, almost thread-like in specimen U.S.N.M. No. 103-906a between the diameters of 4 and 5 mm., now becomes strong, but is only indistinctly serrated, each denticulation corresponding to one rib. There are in this stage 23 ribs per half whorl in specimen U.S.N.M. No. 103913c and slightly fewer in U.S.N.M. No. 103913d. In some individuals, e.g., U.S.N.M. No. 103913g, the ribs are in this stage prorsiradiate to an unusually high degree (pl. 16, fig. 26).

The next, and more important, sculptural change is the rather sudden disappearance of the secondary ribs, at least on the sides. This change occurs, according to speed of development, in various growth stages, viz., at diameters of 25 mm. in the holotype, between 25 and 30 mm. in U.S.N.M. No. 103906b, of 30 mm. in U.S.N.M. No. 103913d, of 35 mm. in U.S.N.M. Nos. 103913b and 103906e, and of 40 mm. in the largest paratype present (U.S.N.M. No. 103913e). (Another individual, U.S.N.M. No. 103913i, however, keeps its dense costation up to its anterior end which corresponds to a diameter of about 34 mm.) For some time after the disappearance of the secondary ribs, up to diameters of about 35 mm. in some individuals and of about 45 mm. in others, faint folds can be seen in the intercostals on the sides. On the venter, however, the secondary ribs, continuing those faint folds, persist much longer. Sometimes, particularly in the holotype, they carry even outer tubercles which are not markedly, or not at all, weaker than those of the primary ribs. The circumumbilical nodes, on the other hand, are restricted to the primary ribs. In some specimens, e.g., U.S.N.M. No. 103906c, these nodes grow, between the diameters of 40 and 50 mm., high and sharp. Seven primary ribs can be counted on the anterior half of the penultimate whorl of the largest paratype (U.S.N.M. No. 103913e), four on the last quarter of its outer whorl, 12 on the outer volution of the holotype, and 13 on that of paratype U.S.N.M. No. 103906b. Simultaneously with the fading of the secondary ribs on the sides the lateroventral tubercles become much more prominent than they were before, forming sometimes blunt knobs, sometimes rather sharp tubercles pointing strictly outward, sometimes just strong swellings which are elongated diagonally toward the keel. In the last case they occasionally absorb the outermost tubercles, as they did in an early stage. In all cases, however, they are far more developed than the latter. This description relates to the stage between the diameters of 35 and 45 mm., studied particularly in specimens U.S.N.M. Nos. 103913b and 103906c. The latter is, moreover, distinguished by large and high teeth which lend its keel the cockscomb-shape characteristic of the typical *P. woollgari*.

The further sculptural development on and

near the periphery between the diameters of 40 and 85 mm. can be studied best in the holotype, paratype U.S.N.M. No. 103906b, and in the penultimate whorl of the largest paratype, U.S.N.M. No. 103913e (pl. 17, figs. 1, 2, pl. 18, fig. 1, pl. 17, fig. 4). At the beginning of this stage the nodes of both outer rows tend to become more or less equal in strength. Those of the outermost row are more distinctly elongated in the spiral sense than the lateroventral ones which, in the holotype, are more knob-like or bullate. Later they become horn-like, occasionally (last but one on right side of holotype, pl. 17, fig. 1) even quite sharp and, once more, much more prominent than the outermost nodes which are at first relegated again to mere spiral ridges on the outer slopes of those horns and disappear entirely, in both the holotype and paratype U.S.N.M. No. 103906b, toward the end of this stage. The development of the keel also can be studied best in this paratype (pl. 18, fig. 1). It is strong and considerably higher than the outer nodes. Its teeth, corresponding in number to the primary ribs, are much longer than the interstices between them and comparatively low. They accentuate a character, recognized in other forms of this species also, by sloping very gently apicad but rather sharply orad, thus causing the notches of the cockscomb to be more marked than its teeth. It may be worth noting that in all three individuals here discussed more or less weak ridges representing the outer ends of greatly reduced or even lost secondary ribs are intercalated between two outer tubercles each but do not carry any nodes themselves. The test, partly preserved on the outer whorl of paratype U.S.N.M. No. 103906b, shows growth striae varying in strength; about 15 of them can be counted between two ribs.

The outer whorl of the largest paratype (pl. 17, figs. 4, 5) exhibits, between the diameters of 98 and about 125 mm., the last sculptural phase observable in this variety, the gerontic one. There are five more or less fold-like, rather straight ribs per quarter whorl. Their circumumbilical tubercles are shifted, as in the late ontogenetic stages of other forms of this species, ventrad as far as the first third of the whorl height. They are pointed near the anterior end of this whorl only. There are, furthermore, strong lateroventral tubercles. Of these, however, only the second from the posterior end is fully preserved. It is compressed and somewhat elongated spirally and carries on its outer slope a slight swelling, reminiscent of the outermost node. No trace of the latter is, however, found on any of the four following "horns." Thirteen more or less faint folds, running at an angle of 45 degrees to the keel, can be counted on the venter between the antepenultimate horn and the last. Ontogenetically, they are vestigial secondary ribs. They can be followed across the keel on which they form hardly perceptible serrations.

Specimen U.S.N.M. No. 103913f, preserved up to a diameter of 38.5 mm., deviates in its ornamentation from the other shells referred to this variety (pl. 16, figs. 28, 33). All its ribs are uniform at their outer ends up to a diameter of about 25 mm. Only later the outer nodes, which just begin to split into lateroventral and outermost ones, are restricted to, or at least more pronounced on, certain ribs. Also, there are altogether fewer ribs, only 19 on the anterior half of the outer whorl. Accordingly they are broader and flatter than in other individuals, and there is never more than one secondary rib intercalated between two primary ones. These differences in ornamentation are, however, considered to be due merely to individual variation. This specimen is therefore left with the variety *praecox* to which most of the individuals associated with it belong, the more so since its rectangular section (pl. 16, fig. 31) perfectly agrees with that of some of the latter.

(G) Var. alata

Three successive sculptural stages of this variety can be studied in the present material. The only representative of the first is the tip of a single horn, belonging to the penultimate, and deeply indenting the interior outline of the outer whorl of the fragment U.S.N.M. No. 103912a (pl. 18, fig. 2). This horn shows clearly the furrow which is believed to indicate the posterior boundary of the rib, recognizable up to the tip of the horn, and which is seen on the horns of the outer volution as well. There is another indistinct groove which might indicate the anterior boundary of the rib.

The second stage is represented by the outer whorl of this fragment which is still septate throughout. There are altogether four ribs, three of them on the last quarter whorl; the two posterior ones are radial, the two anterior ones prorsiradiate in direction. These ribs are high and rather sharp only near their circumumbilical nodes, which they carry at the first third of the sides, but they are clearly recognizable up to the tip of the horns, accompanied anteriorly by the shallow furrow mentioned above. The first and second of these horns are fully preserved, the last almost so; they grow considerably in strength and become gradually more prorsiradiate orad. In ventral view (pl. 18, fig. 7) all these horns point sidewise, but while in the second the posterior margin runs almost perpendicularly to the median plane and the anterior one obliquely forward, the opposite is true in the foremost horn, whose posterior margin runs obliquely backward. The ventral slope of these horns is very gentle, if not horizontal. The keel, where preserved, overtops the peaks of the horns decidedly at the posterior end of this fragment, but only slightly, as it seems, farther orad. It seems to undulate gently. The same is also seen in a scanty fragment from another locality doubtfully referred to this variety (U.S.N.M. No. 103905), which consists merely of a part of the venter with a single, long horn, hardly overtopped by the exceptionally broad and low keel.

In both these specimens growth striae can be recognized. In U.S.N.M. No. 103912a they run across the umbilical wall in a flat, orad concave arch whose chord is distinctly rursiradiate. In U.S.N.M. No. 103905 they form an orad pointing tongue across the keel. In the former individual there may be from 15 to 20 such striae which, in their turn, carry still finer ones, between two ribs.

By way of appendix it may here be mentioned that the only fragment of a large horn found in the block from southern Utah, attached to a specimen (U.S.N.M. No. 103897k) of the variety *regularis*, shows the beginning of a ridge comparable to those indicating the ribs on the horns of this variety. This fragment is, however, too incomplete to be referred to any given form within *P. woollgari* (see pp. 153, 156).

The third stage is represented by a single, rather sharp horn with what is believed to be the left side of the venter of a large disk of about the same size as the holotype (U.S. N.M. No. 103912b, pl. 18, fig. 9). This horn points outward in ventral view, with the posterior margin being apparently more oblique than the anterior one, and strictly sidewise in sectional view. On its lower surface the outer part of the rib can well be seen. In this fragment also it is anteriorly accompanied by a shallow furrow. Its upper surface is at first almost horizontal and then rises toward the inconspicuous keel which seems still to undulate very gently.

Although this fragment can, in sectional view (fig. 22), be well harmonized with Meek's (1876, pl. 6) figure 2, a proper comparison of the sculpture of the specimens here referred to the variety *alata* with that of the holotype would require accessibility of the latter to examination (see p. 152).

SUTURE LINES

As in the preceding section, the shells too young to be assigned to any given form within this species are first dealt with. Among them the minute disk U.S.N.M. No. 103900b exhibits, at a diameter of about 4 mm., just the outlines of the outer suture line on the left side. The inner half of a bifid external saddle, a rather shallow first lateral lobe with apparently three short terminal points, a broad lateral saddle, considerably higher than the external one, and a shallow, semicircular second lateral lobe are recognizable. The following sutural elements can be seen even better, at a diameter of about 5 mm., in specimen U.S.N.M. No. 103900a (fig. 30): the broad external saddle, intersected by a rather short and sturdy, distinctly three-pronged lobule, the wide and shallow, clearly trifid first lateral lobe, the bifid lateral saddle, the indistinctly bifid, broad, second lateral lobe, and on the umbilical wall another saddle and an auxiliary lobe.

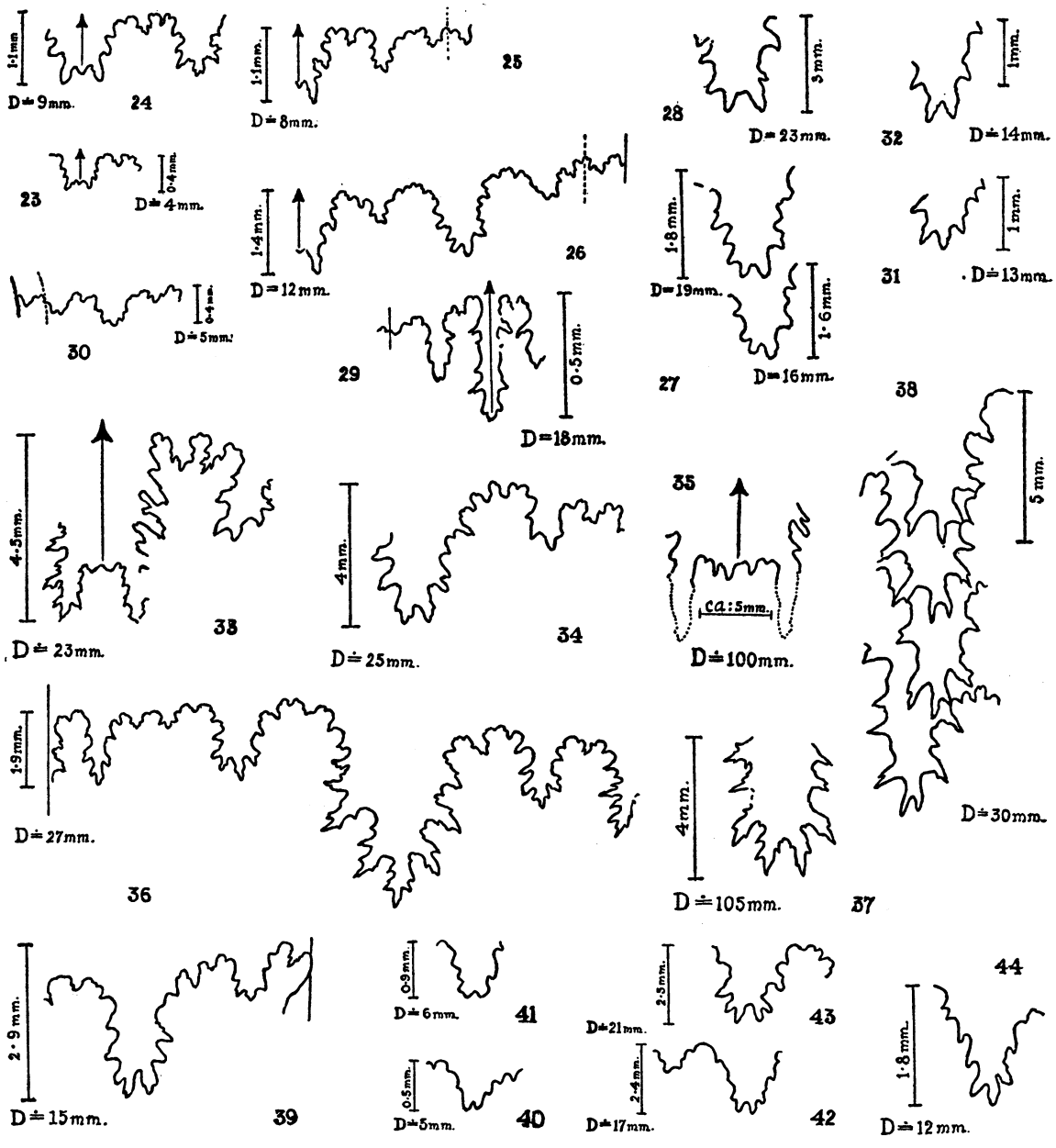
In specimen A.M.N.H. No. 9529/2:1 the suture lines can be studied in about the same stage, viz., between the diameters of 4 and 5 mm., but here it is the ventral part, invisible in the suture lines discussed above, that can be observed best (fig. 23). There is a wide, rather short siphonal lobe, ending in two

but slightly diverging points which are separated by a low, broad-trapezoidal median knob. Even in this early stage the latter can clearly be seen to be indented, or at least a little concave, in the middle. Broad, bifid external saddles flank the siphonal lobe. The same individual shows on its next whorl a more advanced sutural development at diameters of from 7 to 10 mm. (fig. 24). The siphonal lobe is still wide but deeper, and the median knob is deeply indented along the median line. In addition to the terminal points, there are two lateral ones on either side of this lobe. The external saddle is extremely wide, occupying beyond the latero-ventral shoulder almost all of the outer half of the side. It is subdivided by a distinctly three-pronged lobule into two stems, both of which are slightly indented on top. They are about equally broad, but the inner one is higher than the outer. There follows a moderately deep, decidedly trifid first lateral lobe. Of its terminal points the outer one is somewhat stronger than the inner, and the middle one is three-pronged. There are, in addition, two lateral points on either side. The remainder of the outer suture line cannot be seen clearly enough to be described.

(A) Forma typica

Specimen U.S.N.M. No. 103895k has its suture lines exposed on the venter at a diameter of as little as about 2 mm. Already in this very early phase they agree with the description given above of the earliest suture line studied in A.M.N.H. No. 9529/2:1. In specimen U.S.N.M. No. 103895m the sutures can be well studied at a diameter of about 8 mm. (fig. 25), thus supplementing the observations reported above for about the same diameter in specimen A.M.N.H. No. 9529/2:1. There is a short and comparatively slender first lateral lobe; of its three terminal points the outer is more developed than the inner. There follow a very broad, dome-shaped lateral saddle, a short, triangular, second lateral lobe, and another broad and bifid saddle, reaching beyond the umbilical shoulder; an auxiliary lobe is visible on the umbilical wall. The sutural development can be well followed in the same individual beyond the diameter of 25 mm. At 12 mm. diameter (fig. 26) the external saddle is very wide; its inner stem is higher than the outer one. The first lateral lobe is deeper and a little more richly indented along its margins than in the preceding stage, and the difference in strength between its outer and inner terminal points has become more pronounced. It is still shorter than the siphonal lobe. The first lateral saddle is now higher and less broad. The second lateral lobe is less than half as deep as the first and distinctly bifid. There follow a broad and low second lateral saddle, distinctly halved by a three-pronged lobule, a trifid auxiliary lobe, just beyond the umbilical edge, an auxiliary saddle, and another small lobe. Between the diameters of 16 and 19 mm. the transition of the first lateral lobe from trifidity to bifidity can clearly be followed in this individual (fig. 27). Gradual further growth of the outer terminal point until it almost equals the middle one in length, along with a slight dorsad deflection of the lobe as such, and a further upward shift of the former inner terminal point change the trifid lobe into a bifid one at a surprising speed. The final result of this metamorphosis is seen in figure 28, corresponding to a diameter of 23 mm. It is worth noting that in this individual it is the outer point of the first lateral lobe that joins the middle one to produce a bifid lobe, whereas it is the inner one in most of the other shells examined in this respect. This development can well be studied in another specimen, U.S.N.M. No. 103895q, where the first lateral lobe changes from trifidity to bifidity somewhat earlier and even more abruptly, between the diameters of 13 mm. (fig. 31) and 14 mm. (fig. 32).[1]

[1] After what has just been said it may be rather surprising that the suture line represented in Meek's (1876, pl. 7) figure 1e, corresponding, according to my measurements which are supported by Meek's explanation of this figure, to a diameter of about 40 mm., shows a still distinctly trifid first lateral lobe with the outer terminal point stronger than the inner one. However, in the absence of the shell from which this suture line is taken we cannot know to which form within *P. woollgari, sensu lato*, it belongs. Also it must be kept in mind how often asymmetries and anomalies occur in this species (compare, e.g., fig. 89, showing the suture line of the holotype of the variety *praecox* with a decidedly trifid first lateral lobe still at a diameter of 20 mm., although on the right side only). The second lateral lobe, however, seems to be already, though asymmetrically, trifid in Meek's drawing.



FIGS. 23–44. Suture lines of *Prionotropis woollgari* Meek (? *non* Mantell).

23, 24, 30. Shells too small to be assigned to any given form within the species; 23, 24, A.M.N.H. No. 9529/2:1; 30, U.S.N.M. No. 103900a.

25–29, 31–38. *Forma typica;* 25–29, U.S.N.M. No. 103895m (27, 28, to show development of right first lateral lobe; 29, internal suture line); 31, 32, U.S.N.M. No. 103895q, showing rapid change of (left) first lateral lobe from trifidity to bifidity; 33, fragment attached to U.S.N.M. No. 103895c; 34, U.S.N.M. No. 103895r; 35, U.S.N.M. No. 103907c, median knob; 36, U.S.N.M. No. 103895s; 37, U.S.N.M. No. 103907a, right lateral lobe; 38, U.S.N.M. No. 103895t, to show development of (left) first lateral lobe.

39. Var. *crassa*, new variety; holotype, U.S.N.M. No. 103916.

40–44. Var. *intermedia*, new variety; 40–43, paratype U.S.N.M. No. 103896o, to show development of (left) first lateral lobe; 44, paratype U.S.N.M. No. 103896p, left first lateral lobe.

Scale and diameter of disk (D) indicated for each drawing.

The internal branch of the suture line, though somewhat coarsened by weathering, is also well visible in specimen U.S.N.M. No. 103895m, repeatedly discussed above, at a diameter of about 18 mm. (fig. 29). The little lobe beyond the umbilical seam, mentioned above, is followed by a saddle which resembles in both shape and height the auxiliary one, then by a very deep and narrow lobe ending in a two-pronged point, with a lateral one on its internal margin closely above it. This lobe is separated by the high internal saddle, which is intersected by a little lobule on its top, from the narrow antisiphonal lobe. The latter is more than one and one-half times as deep as the preceding lobe and ends in a three-pronged median point. Its lateral margins show distinct points only immediately above the terminal one.

The further sutural development of this form is characterized by increasing richness and fineness of indentation, as shown by the siphonal lobe and adjacent parts of the external saddles of a whorl fragment attached to specimen U.S.N.M. No. 103895c (fig. 33), by the lateral lobes and saddles of another short whorl fragment (U.S.N.M. No. 103895r, fig. 34), and by the inner part of the external suture line and the internal one, taken from a third whorl fragment (U.S.N.M. No. 103895s, fig. 36). All the sutural details illustrated in these drawings correspond to diameters between 23 and 28 mm. It is worth noting that at this stage the second lateral lobe has become decidedly trifid (figs. 34, 36).[1] The internal suture line of specimen U.S.N.M. No. 103895s is particularly interesting for its high degree of indentation, the deep, narrow lobes on both sides of the antisiphonal one having become asymmetrically three-pronged and the internal saddles distinctly bifid. The antisiphonal lobe itself emits three points on either side before ending in a single one.

Excellent preservation permits a close study of the development of the first lateral lobe in four consecutive suture lines of the whorl fragment U.S.N.M. No. 103895t at a diameter of about 30 mm. (fig. 38). Owing to the shift of the outer terminal point up the margin of this lobe, it changes from trifidity to bifidity, but the former middle, now outer terminal point is still markedly longer than the inner. Throughout this development the former is clearly two-pronged, this feature appearing here exceptionally early.

As repeatedly mentioned, there is in this form a wide gap in the sequence of sizes between the diameter of 40 mm. and the largest sizes represented in the material examined. In the ontogeny of the sutures as well as of other characters this gap is bridged by a few specimens only. U.S.N.M. No. 103907a shows on its penultimate whorl, at a diameter somewhat above 40 mm., the same kind of first lateral lobe as just described in a smaller specimen and on its outer whorl a second lateral lobe which is still distinctly bifid, but with the lowest lateral points on either side so close to the terminal ones that it might almost be called quadrufid. All these points are more or less three-pronged (fig. 37).

The fragment U.S.N.M. No. 103907c is remarkable for the very richly and somewhat asymmetrically indented median knob it shows at its posterior end (fig. 35).

By far the most complete suture lines found in any example of *P. woollgari* are excellently visible in the fragment C.N.H.M. No. P5932, here referred to the typical form. This suture line, which may correspond to a diameter of about 140 mm., is but incompletely and inadequately represented in Logan's (1899, pl. 24) figure 2 and is therefore here re-illustrated in figure 45 (see also pl. 13, figs. 4, 19). Here too the median knob, which is comparatively high, is richly but, at least in one of the suture lines, somewhat asymmetrically indented. The siphonal lobe is comparatively deep, with two almost parallel terminal points and two main branches and some minor ones on either side. The external saddles are, as usual in this species, very broad, reaching beyond the ventrolateral shoulder over the outer third of the sides. They are subdivided by a deep, trifid lobule into two main stems, the inner of which is markedly wider than the outer. The former is trifid, though more distinctly so on the right side than on the left; the latter bifid, with a broader inner leaf and a narrower outer one. All these elements are richly denticulated along their margins.

[1] In passing, the remarkable experience may be noted that in many cases a bifid first lateral lobe is linked with a trifid second, and vice versa. If one of these lobes changes in the course of development from one character to the other, the inverse change usually takes place in the other lobe.

The dissymmetry of both sides of this suture line, present in its ventral and ventrolateral portions also, becomes farther dorsad so marked as to require separate descriptions for each side. On the right, the first lateral lobe is considerably deeper than the siphonal one, a little straitened in its upper part, but widely expanding farther beneath. Of its two terminal branches the inner is much longer than the outer. It ends in a long point with four small prongs, arranged in a ventrad ascending order, and carries another, short point at its inner margin. The outer terminal branch in its turn ends in a three-pronged point and carries a short, two-pronged one at its outer margin. These terminal branches are separated by a strong, high, trifid leaf. Another, even stronger one separates the inner terminal branch of this lobe from the four-pronged lowermost lateral point on its inner margin. The first lateral saddle is higher but much less wide than the external one and is intersected by a deep, narrow, bifid lobule. The inner stem of this saddle is considerably broader than the outer, and both are intersected by secondary lobules. The second lateral lobe, situated almost on the umbilical shoulder, attains only about half the length of the first and is on this side clearly and almost symmetrically trifid, with the middle and inner points two-pronged, the outer one indistinctly three-pronged. On the umbilical wall there follows the second lateral saddle, somewhat lower than the external one and deeply laced at about the first third of its height by side branches of the adjacent lobes. At its top it is divided by a three-pronged lobule into a higher and broader outer stem and a lower and more slender inner one. The remainder of the umbilical wall is occupied by a sturdy, almost symmetrically bifid auxiliary lobe which is deeper than the second lateral one and points slightly ventrad. Both its terminal points are two-pronged.

On the left side, however, the first lateral lobe is only a little deeper than the siphonal one and decidedly trifid, with a middle branch that is symmetrically subdivided into two rather short, two-pronged points, and a three-pronged terminal branch on either side. The leaflet separating the outer of these from the middle branch is markedly higher and somewhat stronger than its counterpart on the inner side of this lobe. The first lateral saddle on the left side differs from that on the right by being altogether stouter and much less deeply intersected by the main lobule which is on this side divided into three two-pronged points. Furthermore, the outer stem is here higher and slightly broader than the inner. The second lateral lobe is essentially bifid, with a longer and stronger, two-pronged inner terminal point and a shorter, three-pronged outer one. The latter points obliquely ventrad. Summarizing the differences between the lateral lobes of both sides, it is found that the mature stage, characterized by a bifid first lateral lobe and a trifid second, is reached on the right side of this shell only, whereas on its left the earlier stage, as represented by a trifid first lateral lobe and a bifid second, persists up to a diameter of about 140 mm. Closer examination reveals, however, that the general plan of the second lateral lobe is quite the same on both sides and that a slight ventrad deflection of this lobe, along with some lengthening of its inner terminal point (left side), which thus becomes the middle one (right side), suffices to produce a trifid rather than bifid aspect.

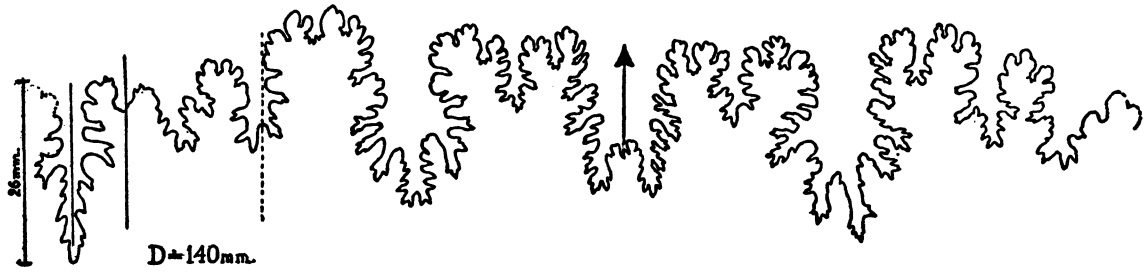


FIG. 45. Suture line of *Prionotropis woollgari* Meek (? *non* Mantell), *forma typica*, C.N.H.M. No. P5932. Note asymmetry. For scale and diameter of disk (D), see figure.

The left second lateral saddle differs from the right merely by being somewhat lower and stouter. The inner leaf at its base, in particular, is more strongly developed. Conversely, the auxiliary lobe is more slender on the left side than on the right, but otherwise hardly different.

The internal suture is seen on the left side better than on the right. The simple, rounded auxiliary saddle is separated from the internal one by a short, simple lobe, but there is no trace left of the small saddle and the deep, narrow lobe which have been found in earlier stages of this species to be intercalated between that lobe and the internal saddle. The latter is halved on its top by a short indentation and intersected on its inner margin by the three side branches of the narrow antisiphonal lobe. The lowermost of these side branches is the strongest and, at least on the left side, clearly two-pronged. There are some minor indentations between it and the long middle branch of the antisiphonal lobe, which is essentially trifid and ends in a tongue-shaped single point.

No usable observations on suture lines could be made in the three giant disks (A.M. N.H. No. 25986) referred with reservation to the typical form. An attempt to make suture lines visible by etching in the largest disk at a diameter of about 140 mm. yielded at first some indistinct outlines which, however, soon disappeared when etching was continued. It seems that most of the septa have been thoroughly destroyed by crushing so as to leave only the outermost septal margins intact which, however, do not stand even a little etching. Furthermore, what seems to be the upper part of the inner stem of a first lateral saddle is incidentally visible in specimen A.M.N.H. No. 25986:2 at a diameter of about 190 mm.

Similarly as it has been done in the discussion of sculptural development, sutural details agreeing with those of the typical form will not be mentioned in the ontogeny of the following varieties, unless necessary for the understanding of specific ontogenetic processes.

(B) Var. **crassa**

In the incomplete holotype parts of the right suture line were exposed on the second volution by removal of the shell (fig. 39). At a diameter of about 15 mm. the first lateral lobe is already distinctly bifid. Its two almost symmetrical terminal points are separated by a slender, upright leaf. The outer point shows a little secondary point at its external margin, thus indicating, even in this early phase, a trend toward becoming two-pronged. The second lateral lobe can clearly be recognized as reaching only a third of the depth of the first and as being symmetrically trifid. These sutural characters strongly support the above (p. 154) assumption of an accelerated development of this variety. Suture lines cannot be studied in the penultimate whorl which is almost entirely covered with the test. Traces found on the outer volution are too poor for any reliable observations.

Since the big paratype U.N.S.M. No. 1-12-12-37 is almost entirely covered with iridescent shell and this fact contributes greatly to its spectacular appearance, the thought of removing the shell for the purpose of suture studies could not be entertained. These studies had to be restricted to the spots where suture lines were visible. This is the case, at first, between the diameters of 60 and 70 mm. Not much can be seen, however, in this stage, except that the first lateral lobe is bifid, with two lateral points immediately above the terminal ones. Furthermore, parts of two subsequent suture lines, from median knob to outer margin of first lateral saddle, can be seen, though not very distinctly, on the right side of the conch near the last septum, at a diameter of about 210 mm. These suture lines may justly be considered the latest and largest ever studied in the present species. What can be seen closely resembles the corresponding parts of the suture line of the whorl fragment C.N.H.M. No. P5932, referred to the *forma typica*, as explicitly described above (pp. 183–185), except that all the visible elements of the external saddle are here considerably sturdier.

(C) Var. **intermedia**

One of the earliest suture lines studied in this variety, that of specimen U.S.N.M. No. 103896j (fig. 46), shows, at a diameter of 12 mm., on the left side a clearly and symmetrically trifid first lateral lobe, whereas on the right side this lobe is considerably longer than

on the left and might be called bifid as well as trifid. The second lateral lobes are strikingly short, the one on the right side attaining only a third of the length of the first, and seem to be just changing from bifidity to trifidity. At about the same size the first lateral lobe is also trifid in specimen U.S.N.M. No. 103896p (fig. 44). In the penultimate whorl of specimen U.S.N.M. No. 103896o, however, this lobe is found to be distinctly bifid, with a comparatively strong lateral point about halfway up its outer margin, as early as at diameters of 5 and 6 mm. (figs. 40, 41). On the outer whorl of the same specimen, at a diameter of 17 mm., is seen a clearly symmetrical bifid lobe with a lateral point on either side immediately above the terminal one (fig. 42). The second lateral lobe is still bifid at this stage. Somewhat later, at a diameter of 21 mm., the first lateral lobe of the last suture line but two is particularly well visible in this shell (fig. 43). It ends in two points, both of which are two-pronged. The perfect symmetry prevailing on the bottom of this lobe is disturbed at about half its height merely by the fact that both the outer leaflet separating the terminal point from the lateral one and the outer lateral point are considerably stronger than their counterparts on the inner margin.

The short whorl fragment U.S.N.M. No. 103896y, believed also to be referable to this variety, might here be mentioned as another example of pronouncedly bifid first lateral lobes and trifid second ones at a diameter as small as 13 mm.

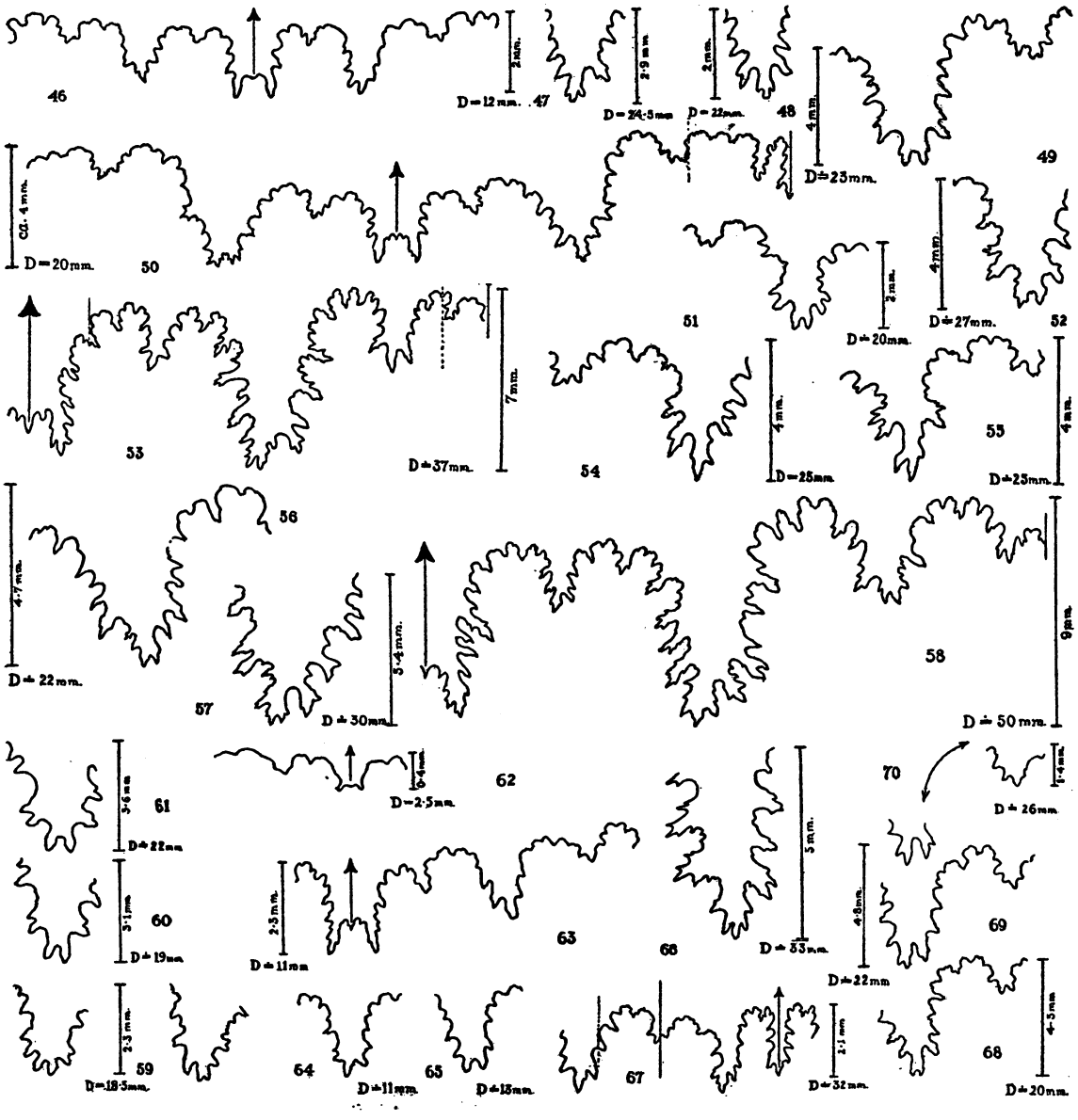
On the other hand, the first lateral lobes are still trifid and the second ones still bifid even in the two last suture lines, corresponding to a diameter of about 20 mm., of the half whorl U.S.N.M. No. 103896a (fig. 51). All three of the terminal points of the first lateral lobe are clearly two-pronged. Trifidity of the first lateral lobe persists even up to diameters of 23 and 24 mm. in specimens U.S.N.M. Nos. 103902d, 103896m, and 103896u. In the first of them the median and the outer terminal points can be recognized to be three- or two-pronged, whereas the inner one is simple and pointed (figs. 47, 48). Thus a certain preponderance of the outer point over the inner, found in other individuals to foreshadow bifidity of this lobe, seems to be indicated in these suture lines also.

Another half whorl (U.S.N.M. No. 103896r) is remarkable for exhibiting, at the diameter of about 20 mm., sutural dissymmetry. Whereas the first lateral lobe is trifid and the second bifid throughout its right side, the former proves to be bifid, with two-pronged terminal points, and the latter trifid on the left side, at least of the anterior quarter of this half whorl (fig. 50). The internal suture line of this specimen closely resembles that of specimen U.S.N.M. No. 103895s of the typical form at a somewhat greater diameter (cf. above, p. 183, fig. 36), except for the fact that the bifidity of the internal saddles is not yet so pronounced.

Another case of dissymmetry is represented by the whorl fragment U.S.N.M. No. 103896l (figs. 54, 55). The first lateral lobe is clearly trifid, with an unusually strong and deep, two-pronged middle point, on the right side (fig. 55), whereas it might be called bifid as well as trifid on the left (fig. 54). Here the main branch is very strong also, but not quite so long as on the opposite side, and ends in a strong point, with a much smaller one at the outer margin. Of the two other points of this lobe the inner is much stronger and longer than the outer. The lateral saddles are but little indented, and the lobules intersecting them are extraordinarily short and blunt. The second lateral lobes are very short and asymmetrically bifid on both sides.

Another first lateral lobe of somewhat aberrant shape is encountered at a slightly smaller diameter in another whorl fragment from the block from southern Utah (U.S.N.M. No. 103896s), but here the difference in length between the two-pronged median point and the two adjacent ones is not so considerable and is, moreover, obscured by the intercalation of secondary prongs (fig. 56).

In the fragments U.S.N.M. Nos. 103896t and 103896w the first lateral lobe is seen to be broad and trifid at diameters of about 23 mm. The middle point is, however, so decidedly two-pronged that one wonders whether this development is not, as it was found in other cases to be (cf. pp. 189, 209, 210), transitional to bifidity. In the first of these fragments the second lateral lobe is rec-



FIGS. 46–70. Suture lines of *Prionotropis woollgari* Meek (? *non* Mantell).

46–58. Var. *intermedia*, new variety; 46, paratype U.S.N.M. No. 103896j; 47, 48, paratype U.S.N.M. No. 103902d, left and right first lateral lobes, to show asymmetry; 49, paratype U.S.N.M. No. 103896t, part of right suture line; 50, paratype U.S.N.M. No. 103896r; 51, paratype U.S.N.M. No. 103896a, part of left suture line; 52, paratype U.S.N.M. No. 103896v, right first lateral lobe; 53, paratype S.D. S.S.M. No. 1672b; 54, 55, paratype U.S.N.M. No. 103896l, left and right first lateral lobes, to show asymmetry; 56, paratype U.S.N.M. No. 103896s, part of right suture line; 57, paratype U.S.N.M. No. 103896x, left first lateral lobe; 58, paratype U.S.N.M. No. 103909e.

59–70. Var. *regularis*, new variety; 59–61, paratype U.S.N.M. No. 103897b, showing development of first lateral lobe, 59, left and right lateral lobes, 60, 61, left lateral lobes; 62–67, paratype U.S.N.M. No. 103897e, 64, 65, left, 66, right first lateral lobes; 68–70, paratype U.S.N.M. No. 103897k, showing development of both right lateral lobes.

Scale and diameter of disk (D) indicated for each drawing.

ognized to be trifid, with a two-pronged middle point (fig. 49).

A similar development of the first lateral lobe as in the fragments just discussed is found in U.S.N.M. No. 103896v at a diameter of about 27 mm. (fig. 52). It differs from that described above in the last septa of U.S.N.M. No. 103896o merely by the fact that the leaflets separating the middle terminal point from the two adjacent ones are more developed than the knob intersecting the middle point, whereas the opposite holds true for U.S.N.M. No. 103896o. This latter relation accounts in other cases for one of the ways of transition from trifidity to bifidity.

However, the trifid stage of the first lateral lobe appears definitely to have been overcome in the largest of the specimens from the block from southern Utah, none of which, however, exceeds 40 mm. in diameter. Septa can be traced up to diameters of about 35 mm. In all of them (e.g., U.S.N.M. Nos. 103896f, 103896g) the first lateral lobe is more or less symmetrically bifid, and the second trifid.

One whorl fragment from the same locality (U.S.N.M. No. 103896x) deserves particular mention for exhibiting, as early as between the diameters of 25 and 30 mm., the highly specialized ramification of the bifid first lateral lobe illustrated in figure 57. The inner terminal branch is longer than the outer and subdivided into a shorter, sharp, inner point and a longer outer one. The outer branch is three-pronged. A strong, slightly dorsad inclined leaf separates these terminal branches. Above the outer one there is the lowermost lateral point of the outer margin which is only a little smaller, distinctly two-pronged and only slightly oblique. This arrangement foreshadows at a surprisingly early stage the one observed in the holotype of the variety *regularis* (fig. 81) and, if some minor differences are neglected, the one found in the fragment C.N.H.M. No. P5932, whose diameter is about six times greater (cf. p. 184, fig. 45).

In the present variety the sutural ontogeny cannot be followed up to the same sizes as in the typical form and in the variety *crassa*. The holotype (S.D.S.S.M. No. 1315), attaining 39 mm. in diameter, is almost entirely covered with shell, and such an exceptionally beautiful example should not be damaged by removing the test for the sake of suture studies. Paratype S.D.S.S.M. No. 1672b, however, which reaches a diameter of 41.2 mm. and which is not quite typical of this variety as to whorl thickness and sculptural character (pp. 165, 176), is septate throughout and splendidly exhibits the external suture line (fig. 53). The siphonal lobe is not so wide and is subdivided by a broad, trapezoidal median knob which shows a deep, pointed middle notch and a shallower one on either side. The external saddle is very broad and rather deeply intersected by a three-pronged lobule which points slightly ventrad. The first lateral lobe is bifid with a two-pronged outer point and a three-pronged inner one, this arrangement being just the reverse of that found in U.S.N.M. No. 103896x, described above. The outer point is longer and markedly stronger than the inner one. The leaflet separating them is asymmetrically subdivided by an indentation which is closer to its outer margin than to the inner one. The first lateral saddle is only half as wide as the external one and intersected on its top by three almost equal lobules. The second lateral lobe attains less than half the depth of the first and is trifid, with the inner point somewhat longer than the outer one.

Of the two medium-sized half disks present in this variety (U.S.N.M. Nos. 103909e and 103911), the first-mentioned exhibits on its outer whorl suture lines corresponding to diameters from 43 to 55 mm. (fig. 58). Although a little corroded, they can be recognized as of about the same type as the one just described. The only increase in indentation is found in the second lateral lobe whose middle point is clearly three-pronged.[1]

Summarizing, the sutural development may well be said to be retarded in many individuals of the variety *intermedia*, as compared to the *forma typica*, to a similar degree as

[1] Merely for the sake of completeness it might be mentioned that in the innermost volution visible in U.S.N.M. No. 103911 the suture lines appear strangely simplified, almost goniatitic, with minute indentations observable at the anterior end of this whorl only, although the diameters amount to from 5 to 12 mm. This curious aspect seems, however, to be due to some incident of preservation rather than to extraordinary retardation of development.

the sculptural one. On the other hand, instances of extraordinarily accelerated development also occur among the individuals here referred to this variety (e.g., U.S.N.M. Nos. 103896o and 103896x). As seen in this heading, there is an almost amazing range of variation in sutural details within this form of *P. woollgari;* no taxonomic significance is, however, granted to it, since there is no sound reason why variation should stop within the limits of a given variety, nor why it should not affect sutural as well as other characters.

(D) Var. regularis

In specimen U.S.N.M. No. 103897e some sutural elements, viz., a bifid external saddle and an apparently trifid first lateral lobe, are recognizable on one of the innermost whorls at a diameter of 1.1 mm., which marks by far the earliest stage at which any sutural observations could be made in *P. woollgari.* The ventral and adjacent parts of the external suture line can be well studied in the following whorl of this conch at a diameter of about 2.5 mm. (fig. 62). Here a wide and shallow siphonal lobe is seen to be subdivided by a low, trapezoidal median knob which is concave at its top. The external saddle is broad, rounded, and intersected by a short, though sharp indentation. The first lateral lobe attains only half the depth of the siphonal one and seems to end in three blunt prongs. In the anterior part of the same volution the first lateral lobe can more clearly be recognized as trifid. Beyond the first lateral saddle a bifid second lateral lobe, a second lateral saddle, and an auxiliary lobe are discernible.

Since suture lines can be studied in this specimen up to its anterior end, it seems advisable to concentrate the study of the sutural development of this variety on this individual first. The external suture lines may be studied particularly well between the diameters of 11 and 14 mm. (figs. 63–65). The median knob is intersected by a remarkably deep and large indentation which is triangular in shape. On the right side of the conch the first lateral lobe is almost symmetrically trifid, with a particularly long median point. On the left side the outer point of the same lobe, which is still clearly trifid at a diameter of 11 mm. (fig. 64), gradually becomes stronger than the inner so that at a diameter of 13 mm. this lobe has become decidedly bifid (fig. 65). Similarly, on the right side of the shell the inner terminal point of the second lateral lobe grows much longer and stronger than the outer, and a secondary prong on its inner margin gradually becomes equal to the outer terminal point. The final result of this change is a clearly and symmetrically three-pronged second lateral lobe.

On this, the right side of the shell, the first lateral lobes remain trifid as long as suture lines are visible, i.e., up to a diameter of 33.5 mm. On the last quarter of the outer whorl this lobe has assumed the shape illustrated in figure 66. There are a broad, three-pronged middle point, varying in length, with two more little prongs immediately above the lateral ones, so that this point might well be called five-pronged in some suture lines, and two more two-pronged terminal points. On the left side of the conch these lobes show at this stage about the same general pattern as on the right, owing to the rather surprising fact that on this side they have turned trifid again at a diameter of about 20 mm. They are, however, less symmetrical than on the opposite side. In contradistinction to what has been observed on this side in an earlier stage, it is now the inner point that always tends to be longer and stronger than the outer, but trifidity seems to be preserved up to the anterior end of this whorl, corresponding to a diameter of about 35 mm. It seems to be in line with the above-mentioned trend of the first lateral lobes to become trifid again, considered a retrogressive development, that the second become temporarily bifid, with two two-pronged points, at least on the right side of the shell. Near the anterior end of this whorl, however, the second lateral lobes are clearly trifid again on both sides of this individual.

On the umbilical wall there follows the rather broad second lateral saddle with two indentations on its outer margin and two more on its top. There is, furthermore, a distinctly trifid auxiliary lobe just riding on the umbilical seam. The internal suture line also is well visible, at a diameter of about 33 mm., in this specimen (fig. 67). There are first a broad, bifid saddle, then a deep and

narrow, asymmetrically three-pronged lobe, separated by the high, bifid internal saddle from the antisiphonal lobe which is somewhat less deep than the preceding one. It ends in a three-pronged point and has two lateral ones on either side. It may be worth noting that the deep, narrow lobes flanking the antisiphonal one are still present (cf. the description of the internal suture line of specimen C.N.H.M. No. P5932, p. 185).

Of other individuals referred to this variety, the whorl fragment U.S.N.M. No. 103897p may here be mentioned for exhibiting, at a diameter of about 10 mm., a clearly visible trifid first lateral lobe (fig. 78), and the specimen S.D.S.S.M. No. 1673a, which shows a clearly trifid first lateral lobe still at a diameter of 22 mm., for its strikingly low saddles and shallow lobes.

The sutural development between the diameters of 12 and 19 mm. can closely be followed in the paratype S.D.S.S.M. No. 1074b. Throughout this phase the first lateral lobe proves to be asymmetrically trifid, the inner terminal point exceeding the outer in both length and strength. The second lateral lobe, which points obliquely dorsad, is also trifid (fig. 71).

Somewhat different is the ontogeny shown between the diameters of 14 and 20 mm. by the whorl fragment U.S.N.M. No. 103897g. Here the first lateral lobe is also trifid, but whereas its middle point is triangular, long, and pointed in the specimen just discussed, it is short, blunt, and two-pronged in the present one. The outer point also is distinctly two-pronged.

In the half disk U.S.N.M. No. 103897k, the change of the first lateral lobe from trifidity to bifidity can be seen to take place, between the diameters of 20 and 26 mm., in the same way as in the typical *P. woollgari* (see pp. 181, 183). In the beginning (fig. 68) there is an undoubtedly trifid first lateral lobe with a symmetrically two-pronged middle point and two more simple terminal points, the inner of which is, however, stronger and slightly longer than the outer. Later the middle point begins to point more and more ventrad, with its inner prong gradually outgrowing the outer one, while the inner terminal point assumes a position symmetrical to it and tends to equal it in length. The outer point moves up the margin of this lobe and dwindles. There results a bifid first lateral lobe, with the inner point still a bit shorter than the two-pronged outer (formerly middle) one (fig. 69). Eventually the inner point, too, becomes asymmetrically two-pronged and almost the counterpart of the other (fig. 70). This development can, however, be followed on the right side of the conch only. On the left the first lateral lobe remains essentially trifid, though with some indication of the transition described above. Simultaneously, the second lateral lobe can be observed to change gradually from bifidity to trifidity on both sides of the shell.

A clearly bifid first lateral lobe with exceptionally long terminal points shows up at a diameter of about 24 mm. in specimen U.S.N.M. No. 103897l (fig. 74). Its suture lines are, moreover, remarkable for the long and slender, three-pronged lobules which separate the lower and narrower outer stems of the external saddles from the higher and broader inner ones.

Whereas the terminal points of the bifid first lateral lobe are simple in the individual just discussed, they are distinctly two-pronged in specimen U.S.N.M. No. 103897n at a diameter of about 27 mm. (fig. 83). They are, however, remarkably longer and more unequal in the right half of this suture line than in the left. Other asymmetries are noticeable in this suture; the right first lateral saddle grows higher than the left, and the second lateral lobe is bifid, with two-pronged points, on the right side, but trifid, with three-pronged points, on the left.

At about the same stage (diameters between 20 and 30 mm.) the first lateral lobes assume, because the leaflet separating the two terminal points is hardly higher than those intersecting them, a four-pronged rather than bifid aspect in some specimens, e.g., U.S.N.M No. 103897m (fig. 72). The second lateral lobes are three-pronged in this individual.

On the right side of paratype U.S.N.M. No. 103903b the first lateral lobes of the last two or three septa (diameter about 29 mm.) are similarly four-pronged, but the leaflet separating the two terminal points is here distinctly higher than the two secondary leaflets that intersect them. This lobe looks still different in the left half of the same

suture line where the middle leaf is, in its turn, indented, and the second prong from the left carries a secondary prong on its inner margin (fig. 73).

A four-pronged first lateral lobe of the type described above changes on the left side of specimen U.S.N.M. No. 103897b, between the diameters of 18.5 and about 22 mm., gradually into a trifid lobe again, with all three branches being two-pronged. This rather surprising change seems to come about by a shift of both outermost and innermost points up the margins of this lobe (figs. 59–61). The material present does not allow a decision as to whether or not this development is really a retrogressive one, as suspected. On the left side, the second lateral lobes are trifid throughout this stage. On the right side, however, the first lateral lobes are asymmetrically trifid with a two-pronged middle point (fig. 59) throughout, and the second ones are bifid.

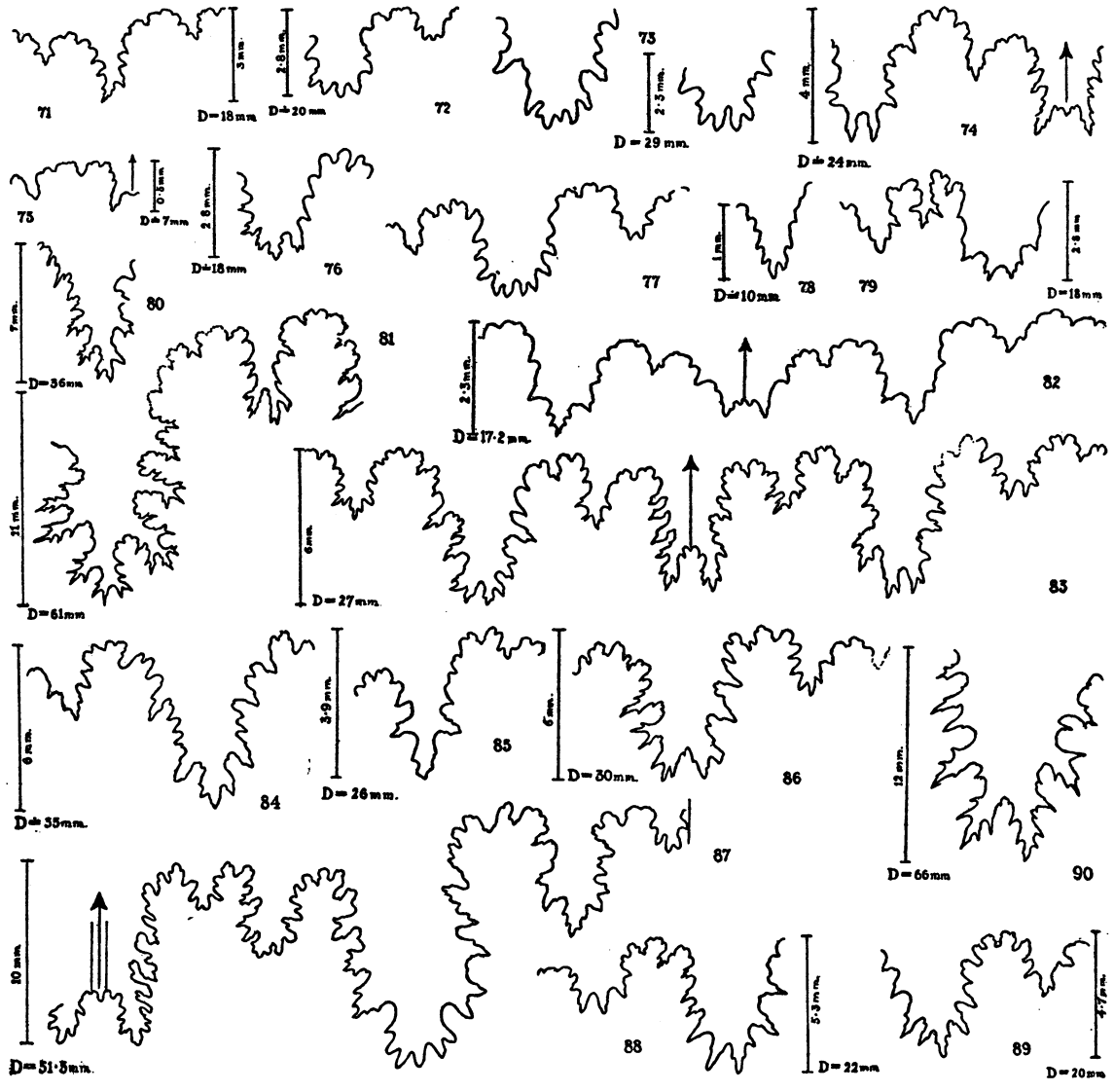
First lateral lobes similar to those depicted in figures 60 and 61 are also found at a diameter of about 24 mm. in the whorl fragment U.S.N.M. No. 103897o.

In the holotype (S.D.S.S.M. No. 1470), which is septate throughout, a slender, asymmetrically bifid first lateral lobe can be seen at a diameter of 36 mm. Both terminal points are three-pronged, as are the lowermost lateral ones on either side (fig. 80). Thanks to the fact that the preceding chambers are filled with crystallized calcite, but the following ones with darker shale, the external saddle and the adjacent lobes are excellently visible at a diameter of 61 mm. on the left side of this shell near the anterior end (fig. 81). The external saddle is broad, as usual, and intersected by a narrow, asymmetrically bifid lobule. Of its two stems the outer is considerably less wide and slightly higher than the inner which in turn is subdivided by a short, three-pronged lobule. The first lateral lobe is comparatively narrow and bifid, with a stronger and longer inner branch and a shorter and more slender outer one which points obliquely ventrad. Both these branches are further ramified. The inner one is divided into a slender inner point and a broad outer one. The latter is almost symmetrically subdivided into two branchlets, both of which are two-pronged. A strong leaf, inclined toward the middle axis of this lobe and slightly indented on both sides, separates the inner branch from the outer. The latter is trifid, with a two-pronged middle point. The same pattern is repeated at a somewhat reduced scale by the lowermost lateral point on the outer margin of this lobe. Altogether this arrangement agrees in the details much better with that found, at less than half the diameter, in specimen U.S.N.M. No. 103896x described and figured above (p. 188, fig. 57) than with that of the fragment C.N.H.M. No. P5932 (see p. 184, fig. 45), which corresponds to a diameter more than twice as great. However, the general picture of intricate ramification of the first lateral lobe, indicating its last stage of development, is the same in all three examples, despite the very considerable differences in size.

In general, the sutural ontogeny of this variety may be said to equal, if not to exceed, the preceding one in both the high degree of variability and the frequency of dissymetric developments. Here, too, the change of the first lateral lobe from trifidity to bifidity seems sometimes to be more or less retarded, as compared with the typical form, and in some cases even retrogressive developments seem to occur.

(E) Var. **tenuicostata**

The earliest sutural stage that can be studied in this rather rare variety is found on the penultimate whorl of the fragment U.S.N.M. No. 103898b at a diameter of about 7 mm. (fig. 75). This suture line follows the familiar pattern of the species. The siphonal lobe is divided by a broad-trapezoidal median knob, which is indented at its top, into two but slightly diverging branches. The broad external saddle is intersected by a triangular lobule; its inner stem is broader than the outer. The first lateral lobe is considerably shallower than the siphonal one and seems to be trifid. Some sutural details are recognizable on the outer whorl of this fragment also, at a diameter of about 18 mm. On the left side (fig. 76) the first lateral lobe is still trifid; of its three terminal points the middle one is three-pronged, the two others are two-pronged. On the right side (fig. 77), however, the first lateral lobe is bifid, with two-pronged



FIGS. 71–90. Suture lines of *Prionotropis woollgari* Meek (? *non* Mantell).

71–74, 78, 80, 81, 83. Var. *regularis*, new variety; 71, paratype S.D.S.S.M. No. 1074b, part of right suture line; 72, paratype U.S.N.M. No. 103897m, part of right suture line; 73, paratype U.S.N.M. No. 103903b, left and right first lateral lobes of same suture line; 74, paratype U.S.N.M. No. 103897l; 78, paratype U.S.N.M. No. 103897p, right first lateral lobe; 80, 81, holotype, S.D.S.S.M. No. 1470, 80, right first lateral lobe, 81, left external saddle and first lateral lobe; 83, paratype U.S.N.M. No. 103897n.

75–77, 82. Var. *tenuicostata*, new variety; 75–77, paratype U.S.N.M. No. 103898b, 76, left first lateral lobe; 82, holotype, U.S.N.M. No. 103904.

79, 84–90. Var. *praecox*, new variety; 79, paratype U.S.N.M. No. 103913j, part of left suture line; 84, paratype U.S.N.M. No. 103913f, part of left suture line; 85, paratype U.S.N.M. No. 103906d, part of left suture line; 86, paratype U.S.N.M. No. 103913d, part of right suture line; 87, largest paratype U.S.N.M. No. 103913e; 88–90, holotype, U.S.N.M. No. 103913, 88, left, 89, right main lobes and saddles, 90, left first lateral lobe.

Scale and diameter of disk (D) indicated for each drawing.

terminal points. The leaflet separating them is only slightly larger than those subdividing them. Thus comes about a four-pronged aspect of this lobe, closely resembling that described above (p. 190) in specimens U.S.N.M. Nos. 103897m and 103903b of the variety *regularis*. The second lateral lobe is symmetrically bifid, but near the anterior end of this fragment, corresponding to a diameter of about 20 mm., a lateral point on the outer margin of this lobe begins to approach the terminal ones in length, a development that might lead to trifidity.

The suture line could be made visible in the whorl fragment U.S.N.M. No. 103898c also, at a diameter of about 12 mm. Here the first lateral lobe is trifid, with a two-pronged middle point; the outer point is markedly longer than the inner. The second lateral lobe seems to be bifid.

Trifid first and bifid second lateral lobes are recognizable in specimen U.S.N.M. No. 103898a also at diameters between 17 and 20 mm.

In the holotype (U.S.N.M. No. 103904) the suture lines are well visible up to the last septum, corresponding to a diameter of 18 mm. Throughout this development the general pattern remains the same (fig. 82). The saddles are broad and comparatively little indented; the lobes are rather wide and shallow. The first lateral ones are clearly trifid up to the end, but those on the right side of this shell exhibit rudimentary inner terminal points, thus indicating, as it seems, a certain trend toward bifidity. Their middle points tend to be three-pronged in the last septate quarter whorl, but not in all suture lines of this portion does this trend come into full display. The second lateral lobes, too, are trifid on both sides. It may be worth noting that the median knobs show, as a rule, two unequal indentations, the shallower one slightly to the left of the keel, the deeper one slightly to its right, with the little knob between them just riding on the keel.

As has been pointed out above (p. 155), this variety may be considered somewhat stunted in its sculptural development. Since ornamentation and suture lines tend in this species to agree more or less in speed of development, it is no wonder that none of the few individuals that could be examined in this respect reaches the advanced ontogenetic stage that is characterized by bifid first lateral lobes.

(F) Var. **praecox**

Of the two specimens of this variety exposing the innermost whorls only U.S.N.M. No. 103913a permits the study of the earliest sutural stages. At a diameter of about 2 mm. an extremely broad, bifid external saddle and a trifid first lateral lobe are recognizable. Toward the anterior end of this fragment, at a diameter of about 26 mm., this lobe is seen to be bifid, with a stronger, two-pronged inner terminal point and a more slender and pointed outer one; the second lateral lobe appears to be trifid.

At the same diameter of 26 mm. the picture is somewhat different in specimen U.S.N.M. No. 103906d. Its last septum (fig. 85) shows a clearly trifid first lateral lobe, with an unusually deep and strong three-pronged middle point, and an extremely short second lateral lobe which is also trifid.

In specimen U.S.N.M. No. 103913j, however, the first lateral lobe is found to be bifid and the second to be trifid as early as at a diameter of about 18 mm. (fig. 79).

Besides U.S.N.M. No. 103913a, discussed above, there is only one more specimen, U.S.N.M. No. 103913d, in which suture lines can be studied in a comparatively early stage. Here, at a diameter of about 7.5 mm., the first lateral lobe can be seen to be triangular in shape and trifid, whereas the second is clearly bifid. In the same individual the last septum, corresponding to a diameter of about 30 mm., is particularly well preserved (fig. 86). The first lateral lobe is bifid, with a three-pronged outer terminal point and a somewhat wider, two-pronged inner one, the second short and trifid.

In this variety as well as in other forms of this polytypic species there is much variation in speed of sutural development. Whereas bifid first lateral lobes have been found as early as at diameters of 18 and 26 mm. in two of the individuals hitherto discussed (U.S.N.M. Nos. 103913j and 103913a), these lobes are still undoubtedly trifid in specimens U.S.N.M. Nos. 103913g and 103906e at

diameters of 20 and 22 mm., respectively. In the former the second lateral lobe is at this stage markedly short and also trifid. In the example U.S.N.M. No. 103913b the first lateral lobes are found to be trifid, and the second bifid, even up to the last septum which corresponds to a diameter of about 34 mm.

The individual U.S.N.M. No. 103913f, stated above (p. 179) to be somewhat aberrant in ornamentation, exhibits some sutural peculiarities also (fig. 84). At a diameter of 35 mm. the first lateral lobe points slightly ventrad and ends in two very unequal points, the inner of which is much stronger and longer than the outer. Higher up on either margin of this lobe are seen two lateral points which are almost symmetrical as to both site and shape. The second lateral lobe of this suture line is symmetrically trifid, with a particularly strong, three-pronged middle point.

The holotype of this variety (U.S.N.M. No. 103913) is remarkable for the dissymmetry between both sides of the conch at diameters between 20 and 22 mm., caused by differences in the rate of development. On the right side the first lateral lobe is still trifid and the second, though asymmetrically, bifid (fig. 89), whereas the opposite holds true of the left side (fig. 88). As a further asymmetry it may be noted that the second lateral lobe is rather slender, though short, on the right side, but particularly wide, and still shorter, on the left. Moreover, the first lateral lobe of one of the last septa of the holotype could be exposed on its left side at a diameter of 66 mm. (fig. 90). It is bifid. Both its terminal points, which are separated by an almost upright, triangular leaf, are three-pronged, but the outer is longer and less oblique than the inner. The former carries a spur at its outer margin and is separated by an oblique, rounded leaf from the slender and three-pronged lower point of the bifid lowermost lateral branch on the external margin of this lobe. Despite certain similarities in the general pattern, this development proves to be different from all those previously studied, viz., in the specimens C.N.H.M. No. P5932, referred to the typical form of this species (p. 184, fig. 45), U.S.N.M. No. 103896x, referred to the variety *intermedia* (p. 188, fig. 57), and S.D.S.S.M. No. 1470, the holotype of the variety *regularis* (p. 191, fig. 81).

In disk C.N.H.M. No. P5931, believed to be referable to this variety, suture lines are visible between the diameters of 27 and 70 mm. Throughout this ontogenetic range the first lateral lobes are bifid, with two long terminal points and two shorter and more diverging lowermost lateral ones, and the second lateral lobes are particularly narrow and trifid. Of all the medium-sized individuals of this variety that could be examined, this is the only one whose sutural elements are as deeply intersected as they are in other forms of *P. woollgari* and thus do not exhibit the simplified character mostly encountered in the variety *praecox* (see below, p. 195).

Finally, suture lines could be studied in the largest paratype present (U.S.N.M. No. 103913e) at diameters of approximately 50 and 100 mm. At the former size (fig. 87) the siphonal lobe, richly indented along its margins, is divided by a comparatively slender median knob whose height amounts to less than a third of the depth of this lobe. It is worth noting that, as similarly observed in a specimen of the variety *tenuicostata* (p. 193, fig. 82), by far the deepest indentation of this knob is not found on top of the keel but on its right slope. The unusually wide external saddle is divided by a wide, trifid lobule with a three-pronged middle point into two stems, the outer of which is almost twice as broad as the inner. The former is intersected by a rather short, trifid lobule with a two-pronged middle point. The first lateral lobe is wide and asymmetrically bifid. Both its terminal points are two-pronged. The leaflet between them is not so much bigger than those intersecting them, so that this lobe might, in some cases at least, be called four-pronged as well (cf. the discussion of the sutural development of the variety *regularis*, pp. 190, 191, figs. 72, 73). On the other hand, the leaflet separating the inner terminal point from the neighboring lateral one is more developed than the middle one. The first lateral saddle is considerably higher than the external one, but only half as broad, and shows only shallow indentations on its

top. The second lateral lobe is distinctly trifid, with a three-pronged middle point. There follow an asymmetrically bifid second lateral saddle and a short, trifid auxiliary lobe with a blunt, two-pronged middle point.

The last septa of this individual are visible, though somewhat corroded, on the preserved part of the outer whorl. The first lateral lobe is now symmetrically bifid, with somewhat diverging, two-pronged terminal points. The second is rather wide and trifid. All three of the terminal points seem to be three-pronged; the inner is stronger and longer than the outer. The sturdy, bifid second lateral saddle separates this lobe from a symmetrically bifid auxiliary lobe on the umbilical wall, whose terminal points are both two-pronged.

With the only exception of those of specimen C.N.H.M. No. P5931, described above, the suture lines of this variety may be said to be characterized by the fact that the indentation of both saddles and lobes, although quite rich for the respective stages, does not intersect these bodies so deeply as in some other forms of this species. This holds true even for the lobules intersecting the main saddles and their stems. This somewhat simplified sutural character of the variety *praecox*, no less than its sculptural habit, causes it to approach most closely the following species (pp. 156, 178, 179) of all the forms

FIG. 91. *Prionotropis woollgari* Meek (? *non* Mantell), var. *alata*, new name; paratype U.S.N.M. No. 103912a; suture line at diameter of about 110 mm., with details of the external saddles of preceding and two following suture lines, to show influence of ornamentation. For scale, see figure.

here referred to *P. woollgari*. Since, furthermore, transition of the first lateral lobe from trifidity to bifidity takes place on an average comparatively late, the sutural development of this variety seems somewhat slow. This statement is quite consistent with the above (p. 156) observations on its sculptural ontogeny, since the acceleration of development, as alluded to in the varietal name, takes place in the later and latest stages rather than in earlier ones.

(G) Var. **alata**

Of the few fragments representing this variety within the present material, only one (U.S.N.M. No. 103912a) exhibits suture lines. The last five of them, approximately corresponding to diameters from 100 to 125 mm., can partly be studied on the right side of this whorl fragment which is septate throughout (fig. 91). The deep and slender siphonal lobe is divided by the roughly rectangular median knob into two almost parallel branches. Their margins are richly indented. Here the notch intersecting the median knob has an exactly median position, riding just on top of the keel. The external saddle is extremely broad, covering beyond the ventrolateral shoulder a full half of the side. Its main lobule is situated just on that shoulder. Its inner main stem is considerably broader and higher than the outer. The main lobules and adjacent parts of the external saddles of the preceding suture line and of the two following ones have been added to the drawing to show how strongly sutural details are affected by the sculpture. The uppermost lobule, which is situated entirely in a flat intercostal, may be considered undistorted. It is the longest and narrowest, and has a three-pronged middle point and two lateral ones on either side. Those on the inner margin are stronger than those on the opposite side. The preceding lobule, which is on the orad slope of a horn, is considerably shorter and slightly deflected dorsad. The next suture line is the one drawn in full; its main lobule is on the apicad slope of the same horn; it is shorter than the first, but longer than the second, and otherwise not distorted. The lowermost lobule, situated on the orad slope of the preceding horn, is not only shorter than both the first and the third, but is strongly deflected ventrad and distorted accordingly. The first lateral lobe is markedly shorter than the siphonal one. It is divided into a shorter and more slender, three-pronged, outer terminal branch and a longer and broader inner one which is in turn subdivided into a short, broad, outer point and a long, slender, three-pronged inner one. The outer point is again subdivided by a low, dome-shaped leaflet into two two-pronged terminal points. Despite the considerable difference in size, this arrangement is essentially the same as in the holotype of the variety *regularis* (see p. 191, fig. 81). The first lateral saddle, too, is very broad, attaining about three-fifths of the width of the external one, and considerably higher than the latter. Of its two stems, which are separated by an irregularly trifid lobule, the inner is a little higher and wider than the outer. The second lateral lobe is more than half as deep as the first and points decidedly dorsad. It has two terminal points, the outer being clearly three-pronged and markedly stronger than the pointed inner one, and a three-pronged lateral point at about half its depth on either side. The second lateral saddle equals the first in height but is much narrower. It shows two minor lobules, the outer of which is two-pronged. Beyond this saddle the outer and middle points of a short auxiliary lobe are visible. The former is two-pronged; the latter, three-pronged.

This suture line differs from Meek's (1876, pl. 7) figure 1h, which illustrates a suture line of about the same size taken from the holotype of this variety, chiefly by the far greater width of the saddles and in the pattern of the first lateral lobe which appears in that drawing more or less symmetrically trifid. Only careful study of the holotype, which is unfortunately inaccessible at present, could reveal to what extent these differences might be due merely to inaccurate representation.

MATERIAL STUDIED; ITS RANGE AND DISTRIBUTION

(A) *Prionotropis woollgari* Meek (? *non* Mantell), *forma typica*

U.S.N.M. No. 103895: About[1] 125 specimens (including fragments) from a block, probably collected by the Powell Survey from the lower part of the Mancos[2] shale in southern Utah ("original data lost many years ago").

U.S.N.M. No. 103894: A little disk from the lower part of the Carlile shale, locality 11190, 2½ miles south of Newcastle, Wyoming, on western rim of Black Hills; collectors, Longwell and Rubey, 1922.

U.S.N.M. No. 103907: Three specimens, viz., a small disk, an incomplete, rather large specimen, and a fragment of another of almost the same size, from the lower part of the Carlile shale, 60 feet above Greenhorn limestone, locality 12665, 1 mile south of Newcastle, Wyoming, on western rim of Black Hills; collector, W. W. Rubey, 1924.

U.S.N.M. No. 103914: A natural mold of a small specimen from the lower part of the Carlile shale, locality 10334, Pedro, 7 miles northwest of Newcastle, Wyoming, Black Hills rim; collector, T. W. Stanton (formerly included in U.S.N.M. No. 32464).

U.S.N.M. No. 9083: A latex cast of a natural mold of a medium-sized specimen from glacial drift, Black Hawk Creek, Black Hawk County, Iowa.

C.N.H.M. Nos. P5932,[3] 5933: Two whorl fragments belonging to large specimens "from the Blue Hill shales of the Benton,"[4] Solomon River, Osborne County, Kansas.

Doubtfully referred to *forma typica*

A.M.N.H. No. 25986: Three crushed giant disks from "Ft. Pierre," probably Benton shale, vicinity of Edgemont, South Dakota; collector, Barnum Brown, 1903.

Transitional between *forma typica* and var. *crassa*

U.S.N.M. No. 103908: A fragment from the lower part of the Carlile shale, 60 feet above Greenhorn limestone, locality 12665, 1 mile south of Newcastle, Wyoming, on western rim of Black Hills; collector, W. W. Rubey, 1924.

(B) *Prionotropis woollgari* Meek (? *non* Mantell), var. *crassa*, new variety

U.S.N.M. No. 103916: One specimen, holotype, from the lower part of the Carlile shale, locality 10334, Pedro, 7 miles northwest of Newcastle, Wyoming, Black Hills rim; collector, T. W. Stanton (formerly included in U.S.N.M. No. 32464).

U.N.S.M. No. 1-12-12-37: A very big specimen from the Carlile shale of north central Kansas, exact locality unknown.

Doubtfully referred to var. *crassa*

A latex cast of a natural mold of a small disk from glacial drift, Black Hawk Creek, Black Hawk County, Iowa, attached to cast U.S.N.M. No. 9083.

(C) *Prionotropis woollgari* Meek (? *non* Mantell), var. *intermedia*, new variety

U.S.N.M. No. 103896: About 80 specimens (including fragments) from the block from southern Utah, mentioned above.

U.S.N.M. No. 103902: Four small specimens from the lower part of the Carlile shale, locality 11190, 2½ miles south of Newcastle, Wyoming, on western rim of Black Hills; collectors, Longwell and Rubey, 1922.

U.S.N.M. No. 103909: Five specimens, viz., three small disks, a natural mold, and a medium-sized half disk, from the lower part of the Carlile shale, 60 feet above Greenhorn limestone, locality 12665, 1 mile south of Newcastle, Wyoming, on western rim of Black Hills; collector, W. W. Rubey, 1924.

U.S.N.M. No. 103911: A medium-sized half disk from lower part of Carlile shale, locality 18872, 2 miles southeast of Fairburn, South Dakota; collector, N. H. Darton, 1898.

A.M.N.H. No. 9529/2: Six specimens (including fragments) from the "Ft. Benton group No. 2," 1 mile east of Evans Quarry, South Dakota.

S.D.S.S.M. No. 1315: One specimen, holotype, probably from the Carlile formation, Black Hills area, exact horizon and locality unknown.

[1] Despite careful checking of all the fragments for their fitting together, there may still be in this group, as well as in the others derived from the block from southern Utah, some that were counted separately, although belonging to the same specimen. Estimates of the totals of specimens were therefore made conservatively.

[2] According to Rankin's (1944, p. 26) recommendation, the name Mancos is here kept as a stratigraphic term.

[3] Suture line figured by Logan, 1899 (pl. 24, fig. 2).

[4] Quoted from Logan, 1899 (p. 213). No horizon is indicated on the Chicago Natural History Museum labels.

S.D.S.S.M. No. 1672: Two paratypes, probably from first ridge above base, Carlile formation, 10 miles east of Hot Springs, South Dakota.

Tentatively referred to var. *intermedia*

Col. Univ. No. 15002[1]: A whorl fragment from the Ft. Benton formation, Cerrillos Mountains, New Mexico; collector, D. W. Johnson.

Referable to either var. *intermedia* or var. *regularis*

A.M.N.H. No. 9530/1: Altogether 18 small specimens from the "Cretaceous No. 2, Ft. Benton group," 5 miles below mouth of Vermilion River, South Dakota; James Hall Collection. These are the specimens described by Hall and Meek (1855, p. 396) as *Ammonites percarinatus*, including the two specimens figured (*ibid.*, pl. 4, fig. 2a, b).

(D) *Prionotropis woollgari* Meek (? *non* Mantell), var. *regularis*, new variety

U.S.N.M. No. 103897: About 55 specimens (including fragments) from the block from southern Utah, mentioned above.

U.S.N.M. No. 103903: Two paratypes from the lower part of the Carlile shale, locality 11190, 2½ miles south of Newcastle, Wyoming, on western rim of Black Hills; collectors, Longwell and Rubey, 1922.

U.S.N.M. No. 103910: Five small disks from the lower part of the Carlile shale, 60 feet above Greenhorn limestone, locality 12665, 1 mile south of Newcastle, Wyoming, on western rim of Black Hills; collector, W. W. Rubey, 1924.

U.S.N.M. No. 103915: A small disk and molds of four more from the lower part of the Carlile shale, locality 10334, Pedro, 7 miles northwest of Newcastle, Wyoming, Black Hills rim; collector, T. W. Stanton (formerly included in U.S.N.M. No. 32464).

S.D.S.S.M. No. 1470: A medium-sized disk, holotype, probably from Carlile formation, Black Hills area, exact horizon and locality unknown.

S.D.S.S.M. No. 1074: Two paratypes, probably from Carlile formation, Black Hills area, exact horizon and locality unknown.

S.D.S.S.M. No. 1673: Thirteen specimens (mostly fragments), probably from first ridge above base, Carlile formation, 10 miles east of Hot Springs, South Dakota.

Transitional between var. *regularis* and var. *tenuicostata*

U.S.N.M. No. 103899: A fragment from the block from southern Utah, mentioned above.

[1] Figured by Johnson, 1903 (pl. 12, fig. 31a–c).

(E) *Prionotropis woollgari* Meek (? *non* Mantell), var. *tenuicostata*, new variety

U.S.N.M. No. 103904: One specimen, holotype, from the lower part of the Carlile shale, locality 11190, 2½ miles south of Newcastle, Wyoming, on western rim of Black Hills; collectors, Longwell and Rubey, 1922.

U.S.N.M. No. 103917: A natural mold from the lower part of the Carlile shale, locality 10334, Pedro, 7 miles northwest of Newcastle, Wyoming, Black Hills rim; collector, T. W. Stanton (formerly included in U.S.N.M. No. 32464).

U.S.N.M. No. 103983: About 20 fragments from the block from southern Utah, mentioned above.

(F) *Prionotropis woollgari* Meek (? *non* Mantell), var. *praecox*, new variety

U.S.N.M. No. 103906: Eight specimens of various sizes from lower part of Carlile shale, locality 12642, Sec. 31, T. 4 S., R. 8 E. [i.e., about 2 miles south of Fairburn], South Dakota (Black Hills rim); collector, W. W. Rubey, 1924.

U.S.N.M. No. 103913: Thirty specimens (including fragments), among them the holotype and the largest paratype, from lower part of Carlile shale, locality 18872, 2 miles southeast of Fairburn, South Dakota; collector, N. H. Darton, 1898.

C.N.H.M. No. P5931[2]: A medium-sized specimen "from the Blue Hill shales of the Benton,"[3] Solomon River, Osborne County, Kansas.

(G) *Prionotropis woollgari* Meek (? *non* Mantell), var. *alata*, new name

U.S.N.M. No. 103912: Two specimens, viz., a large whorl fragment and a single horn, from lower part of Carlile shale, locality 18872, 2 miles southeast of Fairburn, South Dakota; collector, N. H. Darton, 1898.

Doubtfully referred to var. *alata*

U.S.N.M. No. 103905: Fragment with horn from lower part of Carlile shale, locality 12642, Sec. 31, T. 4 S., R. 8 E. [i.e., about 2 miles south of Fairburn], South Dakota (Black Hills rim); collector, W. W. Rubey, 1924.

Doubtfully referred to either *forma typica* or var. *alata*

A single horn to which the specimen U.S.N.M. No. 103897k referred to the variety *regularis* is attached, from the block from southern Utah, mentioned above.

[2] Figured by Logan, 1899 (pl. 24, fig. 1).

[3] Quoted from Logan, 1899 (p. 213). No horizon is indicated on the Chicago Natural History Museum label.

(H) *Prionotropis woollgari* Meek (? *non* Mantell)

Specimens representing too early ontogenetic stages to be referred to any definite form within this species:

U.S.N.M. No. 103900: About 45 specimens from the block from southern Utah, mentioned above.

TOTAL: About 450 specimens.

As seen from the above list, the occurrences of all the various forms of this polytypic species examined in the course of the present investigation are concentrated geographically in and around the Black Hills region of South Dakota and Wyoming, but they radiate from there as far as from 500 to 600 miles to the southeast (north central Kansas), the south-southwest (Cerrillos Mountains, New Mexico), and the southwest (southern Utah). Precise horizon data, where available, indicate throughout the lower part of the Carlile shale, or Mancos shale, respectively. The specimens of the South Dakota State School of Mines from 10 miles east of Hot Springs, South Dakota, in particular, were collected from the first ridge above the base of the Carlile formation.

As to the distribution of the various forms of this species within the given geographic and stratigraphic range, it may be worth noting that the varieties *praecox* and *alata* appear to be concentrated in only a few of the localities listed. The variety *praecox* occurs within the Black Hills area only in localities 12642 and 18872, about 2 miles south and southeast, respectively, of Fairburn, South Dakota, and is furthermore respresented by a single specimen from Solomon River, Osborne County, Kansas. The variety *alata* occurs in the same two localities of the Black Hills region. According to Meek (1876, p. 457), its holotype is from the "southeast base of the Black Hills, Dakota" or, for all practical purposes, from the same vicinity. Unless the single horn to which specimen U.S.N.M. No. 103897k is attached should prove to belong to the variety *alata*, neither of these varieties is represented in the block from southern Utah which may otherwise be considered the most complete association of the various forms distinguished within *P. woollgari*. (The absence of the variety *crassa* does not prove much, since only two specimens can with certainty be referred to this rare variety.) On the other hand, no other forms than the varieties *praecox* and *alata* are represented at locality 12642, and just one specimen of the variety *intermedia* is associated with them at locality 18872. Only careful collecting in the future can be expected to make clear whether this apparent geographic isolation of the varieties *praecox* and *alata* is a real one or merely due to incidentals of collecting. In the meantime they have, as the other forms of *P. woollgari*, been treated as varieties rather than as subspecies in the present report.

Stratigraphically, however, all the forms listed have to be considered contemporaneous, since even the varieties *praecox* and *alata* are in one locality (18872) associated with the variety *intermedia* which in turn repeatedly occurs together with the *forma typica* and the varieties *regularis* and *tenuicostata*, and since all three of the last-mentioned forms are associated in one locality (10334) with the variety *crassa*.

PRIONOCYCLUS WYOMINGENSIS MEEK

SYNONYMY AND INTRASPECIFIC VARIATION

Ammonites serrato-carinatus MEEK, 1870, p. 429.

Ammonites (*Pleuroceras* ?) *serrato-carinatus* Meek; MEEK, 1871, p. 298.

Prionocyclus wyomingensis MEEK, 1876, p. 452, footnote.

Prionocyclus wyomingensis Meek; WHITE, 1880,[1] p. 35, pl. 15, fig. 1a–e.

Prionocyclus wyomingensis Meek; WHITFIELD, 1880, p. 440, pl. 14, figs. 1–3.

Prionocyclus wyomingensis Meek; STANTON, 1893, p. 171, *cum synon.*, pl. 40, figs. 1–4.

Prionocyclus wyomingensis; GILBERT, 1896, p. 565, pl. 58, figs. 1–3.

Prionocyclus wyomingensis Meek; LOGAN, 1898, p. 463, pl. 106, figs. 1–4.

Prionocyclus wyomingensis Meek; JOHNSON, 1903, p. 139.

? ? *Prionocyclus wyomingensis* Meek; SHIMER AND BLODGETT, 1908, p. 66.

S.[2] *wyomingensis* Meek; GRABAU AND SHIMER, 1910, p. 228, fig. 1510a–d.

Prionocyclus wyomingensis Meek; ROMAN, 1938, p. 457, pl. 46, fig. 435.

Cf.: *Pervinquieria* cf. *romeri* Haas; HAAS, 1943, p. 1, figs. 1–3.

P. wyomingensis Meek; SHIMER AND SHROCK, 1944, p. 593, pl. 247, figs. 3–5.

Mere mentions of the species in faunal lists or otherwise in geological papers, unless accompanied by illustrations, have not been included in the synonymy.

(A) Forma typica

Plate 18, figures 3–6, plate 19, figures 8–10, plate 20, figures 1, 2, 5; text figures 93–97

Meek named this species originally (1870, p. 429) *Ammonites serrato-carinatus*, and a little later (1871, p. 298) *Ammonites* (*Pleuroceras?*) *serrato-carinatus*, simultaneously proposing the generic name *Prionocyclus* for it, but in 1876 (p. 452, footnote), having meanwhile found out that this specific name was preoccupied by Stoliczka (1865, p. 57), he changed it to *wyomingensis*. However, he never figured his species. Its first more precise descriptions and illustrations were published almost simultaneously and, as it seems, independently of each other, by White on the one hand and by Whitfield on the other (see synonymy). White (1880, p. 36, penultimate paragraph) stated his specimens to be Meek's types. Thus there cannot be any doubt that the shells from Medicine Bow River, Wyoming (U.S.N.M. No. 7729), described and figured by White (*loc. cit. in synon.*) and refigured again and again by Stanton, Gilbert, Logan, Grabau and Shimer, Roman, and Shimer and Shrock (for references see synonymy), but not those from the East Fork of Beaver Creek, Black Hills, South Dakota (U.S.N.M. No. 12283), described and figured by Whitfield (*loc. cit. in synon.*), have to be considered typical of Meek's species. The former are, therefore, listed in the United States National Museum type catalogue (1905, p. 535) as "cotype,"[3] the latter (*ibid.*) as "plesiotypes." However, it might be cautious formally here to designate all three of the specimens illustrated by White (1880, pl. 15) in figure 1a, 1b, and e, and 1c and d, as lectosyntypes of the typical form of *Prionocyclus wyomingensis* Meek.

(B) Var. elegans, new name

Plate 19, figures 1–7, 11–14, plate 20, figure 4, plate 21, figures 1–3, 5, plate 22, figures 1, 2; text figures 98–104

The above designation of types for the *forma typica* appears the more necessary since careful comparison proves that Whitfield's specimens are not fully identical with Meek's types which show hardly any costation on the innermost whorls. This character seemed so important to Meek that he stressed it in his subgeneric diagnosis of *Prionocyclus*,

[1] Dr. John B. Reeside, Jr., kindly called my attention to the fact that White's "Contributions to invertebrate paleontology," nos. 2–8, were published as an advance print in July, 1880, three years before the volume containing Part I of the "Twelfth annual report of the United States Geological and Geographical Survey of the territories: A report of progress on the exploration in Wyoming and Idaho for the year 1878" was issued (cf. Nickles, 1923, p. 1093).

[2] Obviously a misprint for "*P.*" (=*Prionocyclus*).

[3] The use of the singular with regard to White's specimens seems to be a misprint.

sensu stricto (1876, p. 453: "Shell, when very young, with costae obscure, . . . "), in contradistinction to *Prionotropis*, whose subgeneric diagnosis Meek (*loc. cit.*) begins with the words: "Shell, when very young, with costae sharply defined, ..."[1] However, in both of Whitfield's individuals, particularly in the smaller one (pl. 14, fig. 1), the ribs are sharply defined even on the earliest whorls visible in the figure, and the costation is dense and fine. This character of the ribbing persists up to the greatest size present in the material examined, corresponding to a diameter of about 90 mm. Also the tubercles, though quite distinct in some specimens, never grow strong in this variety. Furthermore, it is, at least in its later stages (at diameters between 50 and 90 mm.), decidedly more slender than the typical form. The new name *elegans* is here proposed for this variety, and the specimen represented in Whitfield's (1880, pl. 14) figures 1 and 2 is designated as its holotype.

(C) Var. **robusta**, new variety

Plate 20, figures 3, 6, 7, plate 21, figures 4, 6, plate 22, figures 3–5, plate 23, figure 2; text figures 92, 105–107

There is a third form represented in the material studied which deviates from the typical form, and even more from the variety *elegans*, by being almost fully evolute, by having sturdy whorls, much fewer and stronger ribs, and particularly robust circumumbilical and external tubercles, the latter being twin nodes. These distinctive features are best developed at diameters up to 150 mm., whereas in later stages the differences from the *forma typica* are less marked. This hitherto undescribed form is here named variety *robusta*, and the specimen A.M.N.H. No. 25928:2 is designated as the holotype, with A.M.N.H. Nos. 25928:1, 9528/1, and 9528/3 as paratypes.

(D) **Incertae sedis**

Plate 23, figures 1, 3, plate 24, figures 2, 3; text figure 108

In addition, there are three fragments of large shells from Valencia County, New Mexico, which must to a certain extent be considered *incertae sedis* within, or perhaps without, this species. U.S.N.M. No. 103676 comprises two not connecting whorl fragments, the smaller of which, corresponding at its anterior end to a diameter of about 150 mm., might well be referred to the typical *P. wyomingensis*. The larger one, however, attaining a diameter of at least 250 mm., deviates from the equivalent stage of the typical form, as represented by U.S.N.M. No. 103677 from the Carlile shale of Campbell County, Wyoming, by the stronger development of the outer horns. This fragment might be considered transitional between the *forma typica* and the variety *robusta*, or it might represent still another, hitherto unknown variety of this polytypic species. The third specimen is the fragment previously (Haas, 1943) described and figured under the wrong name "*Pervinquieria* cf. *romeri* Haas." It may correspond to a diameter between 200 and 250 mm. At first sight it agrees, even better than does U.S.N.M. No. 103676, with the corresponding stage of the typical form, but its costation is considerably less dense and its whorls are thicker. This fragment can only doubtfully be referred to Meek's species. It might represent still another variety of it or a closely related species.[2]

[1] As a matter of fact, the shells are smooth in the very earliest stages of the type species, *Prionotropis woollgari* Meek (see pp. 168–180).

[2] In a letter dated April 13, 1943, Dr. J. B. Reeside, Jr., suggested that this fragment might be a large adult of a *Prionotropis* like *P. hyatti* Stanton (1893, p. 176, pl. 42, figs. 5–8). Since, however, the true *Prionotropis* of this size develop much stronger tubercles, I prefer to assign this individual to the genus *Prionocyclus*.

ONTOGENY

DIMENSIONS[a]

Specimen No.	D	H	H′	W	W′	U
			(A) *Forma typica*			
A.M.N.H. 25926:1	34.8 mm.	43½	40½	29	31½	29
A.M.N.H. 25926:2	42.2	40½	?	?	30	28½
A.M.N.H. 25926:3	65.9	38	35	29½	31	34½
U.S.N.M. 7729a[b]	64.4	43	?	?	31	29½
U.S.N.M. 7729b[c]	111.0	?	?	?	28½	?
U.S.N.M. 7729c[d]	*ca.* 117	?	?	?	?	*ca.* 42
A.M.N.H. 25926:4	134.0	*ca.* 33½	*ca.* 32	24½	27	43½
U.S.N.M. 103677	275.0	32½	31	24	26	*ca.* 42½
			(B) Var. *elegans*[e]			
A.M.N.H. 25503:3	36.6 mm.	39[f]	36½[f]	?	23½[f]	33
A.M.N.H. 25503:1	37.8	36½	33½	?	28½	36½
A.M.N.H. 25503:2	*ca.* 38.5	38½	*ca.* 32	?	*ca.* 30	*ca.* 35½
Col. Univ. 10630a	40.0	36	?	?	*ca.* 27½	35
U.S.N.M. 12283a[g] (holotype)	41.5	44	?	?	30	31
A.M.N.H. 25503:4	50.7	38½	34	?	26	30
S.D.S.S.M. 1674a	54.6	50	43	?	30	24
U.S.N.M. 12283b[h]	73.3	36	?	?	?	35
A.M.N.H. 25503:5	74.9	40½	35½	?	25½	31½
Col. Univ. 10630b	76.8	41½	37½	?	25	30
A.M.N.H. 25912:4	90.8	38	*ca.* 34	?	*ca.* 26½	33½
S.D.S.S.M. 1507	91.3	38	32½	?	22½	33
			(C) Var. *robusta*			
A.M.N.H. 25928:1	72.1 mm.	34½	*ca.* 32½	*ca.* 28	*ca.* 33½	41
A.M.N.H. 9528/1	137.0	35½	34½	?[i]	?[i]	45½
A.M.N.H. 25928:2 (holotype)	185.0	34	34	*ca.* 29	*ca.* 35	*ca.* 43½

[a] For explanation of symbols, see p. 157.
[b] Measurements from White's (1880, pl. 15) figure 1c, d.
[c] Measurements from White's (1880, pl. 15) figure 1b.
[d] Measurements from White's (1880, pl. 15) figure 1a.
[e] Owing to the density of costation the intercostal width could not be measured in any specimen of this variety.
[f] Measured at D=36.0 mm.
[g] Measurements from Whitfield's (1880, pl. 14) figures 1, 2.
[h] Measurements from Whitfield's (1880, pl. 14) figure 3.
[i] Specimen crushed.

The following inferences may be drawn from the above table:

1. Throughout this species the degree of involution tends, in general,[1] to increase during the earlier part of development, viz., up to diameters between 60 and 80 mm., then to decrease, particularly in maturity. The latter trend may be observed in many ammonite genera ("egression of the spiral"; cf. Haas, 1942c, p. 213, footnote 1); that it cannot fully be observed in the variety *elegans* seems to be because apparently no full grown individuals referable to this variety are present.

2. In the variety *elegans* as well as in the typical form a certain trend toward decrease in the thickness of the disks is also noticeable.

3. At first glance specimens of the variety

[1] The lectosyntype, as shown in White's (1880, pl. 15) figure 1c, is exceptionally involute.

elegans appear to be less evolute than typical ones of the same size. This appearance is, however, deceptive and seems to be caused by the finer ornamentation of the variety *elegans*. As seen from the table, the average degree of involution is even somewhat higher in the typical form than in that variety. This holds true also for a comparison of White's figure 1c and Whitfield's figure 1. Specimen S.D.S.S.M. No. 1674a is exceptionally involute; since, however, all the other characters of the variety *elegans* are well recognizable, this individual was referred to it.

4. The table confirms that, on an average, the disks are slightly thinner in the variety *elegans* than in the typical form, and that they are decidedly thicker in the variety *robusta* than in the two other forms.

5. If the exceptionally thick individual A.M.N.H. No. 25926:3 is left out of account, the ratio W′:H increases gradually in the typical form, except for the largest disk (U.S.N.M. No. 103677), in which it is slightly lower than in the largest but one (A.M.N.H. No. 25926:4). This agrees fairly well with White's (1880, p. 35) statement relative to this matter. In the variety *elegans*, however, this ratio gradually decreases, as far as development can be followed, if the exceptionally thin individual A.M.N.H. No. 25503:3 is here left out of account. This observation contradicts Whitfield's (1880, p. 440) statement to the contrary, apparently based only on the two specimens figured by him, the larger of which happens to have exceptionally low whorls. In the variety *robusta* W′ nearly equals, and sometimes even exceeds, H. This is, however, due merely to the strength of the tubercles in this variety. Where the intercostal width (W) could be measured, it amounts only to 81 per cent and 85 per cent, respectively, of H. Also the ratio W : H increases in the course of development, as does that of W′:H, in this variety as well as in the *forma typica*. The ratios of both intercostal and costal width of the whorl, as compared to its height, have also been measured in the whorl fragment A.M.N.H. No. 9528/3 (not included in the table of dimensions). At its posterior end (pl. 21, fig. 4), corresponding to a diameter of about 110 mm., W′ attains even 106½ per cent of H, but only 99 per cent at the anterior one, corresponding to a diameter of about 135 mm. The ratio W : H also decreases from the posterior to the anterior end of this fragment, amounting to 95 per cent at the former, but only to 81 per cent at the latter.

ESTIMATE OF FULL SIZE

(A) Forma typica

All but one of the measured specimens referred to the typical form prove to be septate throughout. Only in the largest disk present (U.S.N.M. No. 103677; pl. 20, figs. 1, 3, 5) is the last septum clearly seen at a diameter of 250 mm. Assuming a length of the body chamber between one-half and three-quarters of a whorl, the complete disk may conservatively be estimated to have attained a diameter between 400 mm. and 450 mm., by far exceeding the "diameter of coil little if any less than twenty-five centimeters," as assumed by White (1880, p. 36).

(B) Var. elegans

In some specimens of this variety the last septum could be located at diameters between 23 mm. and 80 mm.; not all of these shells, however, are believed to belong to adult individuals. The others are septate throughout, as are the two largest disks referred to this variety, which attain diameters slightly above 90 mm., and a half disk of a somewhat greater diameter. Thus no reliable inferences can be drawn as to the full size reached by this variety. With regard to its more delicate build it may be assumed not to have attained that of the typical form. Whitfield's (1880, p. 440) mention of "a medium or large size" of his form is of no avail. From his explanation of plate 14, which calls the original of his figure 3, measuring not quite 75 mm. in diameter, "a larger individual," it might be inferred that his material hardly included much larger ones, certainly none comparable in size to the specimen U.S.N.M. No. 103677, referred to the typical form.

(C) Var. robusta

Of the three full disks referred to this variety, the two larger ones permit locating the last septum, viz., at diameters of about 90 mm. and 110 mm., respectively, whereas the whorl fragment A.M.N.H. No. 9528/3,

mentioned above, whose anterior end corresponds to a diameter of about 135 mm., is septate throughout. In both those disks almost three-quarters of the outer whorl belongs to the body chamber; thus they seem to be not far from complete, although the apertural margin cannot be seen. Should the larger disk (A.M.N.H. No. 25928:2, holotype) belong to a mature individual, as it seems to do, the diameter attained by this variety may conservatively be estimated at almost 200 mm.

(D) Incertae sedis

The large whorl fragment U.S.N.M. No. 103676, which may be transitional between the *forma typica* and the variety *robusta*, is septate up to its anterior end which corresponds to a diameter of at least 250 mm. The disk may therefore be assumed to have reached the same respectable size as did individuals of the typical form. About the same may hold true of the form represented by the whorl fragment A.M.N.H. No. 25469 which is also septate up to its anterior end, corresponding to a diameter of nearly 250 mm.

WHORL SECTION

(A) Forma typica

The young of the typical form, e.g., A.M.N.H. No. 25926:1 (pl. 18, fig. 4), show a rectangular whorl section. The sides are flat, the venter is truncate, the umbilical wall almost perpendicular; both umbilical and lateroventral shoulders are marked, though rounded. At a diameter of about 100 mm. the sides begin to be slightly vaulted and to converge ventrad, thus changing the rectangular section to a subtrapezoidal one (A.M.N.H. No. 25926:4, pl. 19, fig. 10). Owing to the development of strong circumumbilical nodes, the costal section tapers more distinctly ventrad than the intercostal one. The umbilical wall becomes a little less steep, whereas the venter remains truncate. Two shallow furrows become more and more pronounced on both sides of the keel, also in intercostal section. The keel, where preserved, still considerably overtops the external nodes. In the outer whorl of the largest specimen present (U.S.N.M. No. 103677, pl. 20, figs. 1, 5) the difference between costal and intercostal sections has become much more pronounced than in the earlier stages, owing to the disappearance of the secondary ribs. In intercostal section the sides converge distinctly ventrad, but, here again, they are only gently vaulted, less so than they seem to be in the penultimate whorl of this shell. The costal section appears at first sight almost rectangular, chiefly owing to the external "horns"; there is, however, still some ventrad convergence of the sides visible in this section also, which thus proves to be subtrapezoidal. The venter is still decidedly truncate, but it lacks distinct furrows. The keel is somewhat higher than the horns. Toward the end of this whorl the umbilical shoulder becomes less pronounced, and the umbilical wall less steep.

(B) Var. elegans

In the young, e.g., A.M.N.H. Nos. 25503:2, 25503:3 (pl. 19, figs. 7, 3) the section agrees fairly well with that of specimens of the same size (up to diameters of about 40 mm.) of the typical form. At diameters between 40 mm. and 50 mm. the sides begin to converge ventrad and to become gently vaulted. The section would almost appear oval but for the ventrolateral edges, which remain pronounced, and the venter, which remains decidedly truncate (specimens A.M.N.H. No. 25503:4, pl. 19, fig. 14, A.M.N.H. No. 25912:2, pl. 20, fig. 4), as long as the development can be followed. The umbilical shoulder, however, becomes gradually less marked, and the umbilical wall less steep, between the diameters of 45 mm. and 90 mm. The keel clearly overtops the external nodes and, from a diameter of about 45 mm. on, is accompanied by distinct, though shallow furrows (A.M.N.H. No. 25912:4, pl. 21, fig. 2).

(C) Var. robusta

Within the morphologic range of the species the whorl section seems to be subject to the least ontogenetic changes in the three full disks referred to this variety. Throughout development, so far as it could be studied, the costal section is about as wide as high and subtrapezoidal. The venter is decidedly truncate and broad, but while at the beginning of the last whorl of the holotype (A.M.N.H. No. 25928:2) the keel is still considerably

higher than the peripheric nodes (pl. 22, fig. 3), it is overtopped by the latter at its anterior end (fig. 92). In the whorl fragment A.M.N.H. No. 9528/3, however, the keel is considerably higher than the outermost tubercles and accompanied by distinct furrows. Also the sides are much more vaulted in this fragment which is, moreover, remarkable for showing hardly any impressed zone, thus indicating an almost fully evolute conch (pl. 21, fig. 4). In all the specimens referred to this variety the umbilical shoulder is distinct, though rounded. The umbilical wall seems to be almost perpendicular up to a diameter of about 120 mm., but to decrease in steepness later.

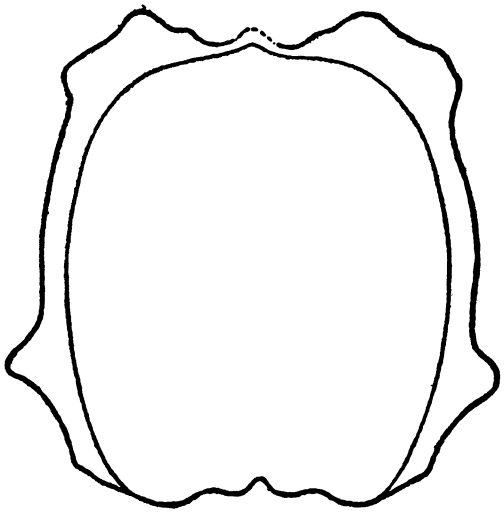


FIG. 92. Whorl section of *Prionocyclus wyomingensis* Meek, var. *robusta*, new variety; holotype, A.M.N.H. No. 25928:2; natural size.

(D) Incertae sedis

In the large fragment U.S.N.M. No. 103676 the whorl section agrees fairly well with the equivalent stage of the typical form, as described above, except for the fact that the costal section is affected by the stronger development of the external horns which, near the anterior end, markedly exceed the keel in height. The fragment A.M.N.H. No. 25469 (Haas, 1943, fig. 3) exhibits a somewhat wider and more convex intercostal section and a costal one with slightly more vaulted sides than the largest disk referred to the typical form.

ORNAMENTATION

(A) Forma typica

Within the present material the ornamentation could be studied from a diameter of about 5 mm. on, but at this early stage on the inner parts of the sides only. They exhibit about six fold-like, straight, prorsiradiate ribs per quarter whorl. These ribs are distinctly thickened at the umbilical edge, where they seem to turn markedly orad, and reach farther down the umbilical wall. At a diameter of about 7 mm. these folds are still recognizable, though much less distinctly than before. At this stage they may justly be called "obscure," as they were by Meek (1876, p. 453) and as they are also seen to be in White's (1880, pl. 15) figure 1c. They are still rather faint at a diameter of a little more than 10 mm., but become then again more and more distinct; at this stage 28 can be counted on a whorl. Their course is still straight and distinctly prorsiradiate on the sides, whereas they rise in a rursiradiate direction across the umbilical wall.[1] At the lateroventral edge they turn sharply forward and then continue, gradually vanishing, on the venter, ending at a short distance from the median keel. The intervals between these ribs vary in width; all are not equally strong, but no regular alternation of primary and secondary ribs can be recognized until a diameter of 30 mm. is reached. At first almost all the costae, then only the primary ones, carry circumumbilical nodes which are elongated in a radial or slightly prorsiradiate direction and tend to become gradually more prominent. Secondary ribs either branch off the primary ones at the ventrad ends of these nodes or are intercalated at about the first third of the sides. The point where the ribs cross the lateroventral edge is marked by another node which tends to be elongated in a spiral, or obliquely spiral, sense. As soon as differentiation between primary and secondary ribs becomes pronounced, only the former carry distinct outer tubercles, whereas these are only slightly indicated or are entirely missing in the latter. Occasionally two ribs originating from one umbilical tubercle also

[1] White's (1880, p. 35) observation that the costae "become obsolete upon the umbilical side" could not be verified.

join the same external one. Between the diameters of 15 mm. and 30 mm., occasionally still at 35 mm., a third row of nodes can be observed beyond the lateroventral shoulder, somewhat nearer to it than to the median keel. These nodes are narrow and not prominent, though distinct, and elongated in a strictly spiral sense. However, this feature of external twin nodes, already mentioned by Meek (1870, p. 430) in the first description of this species, and so much more marked in the early stages of *Prionotropis woollgari*, soon vanishes, only to reappear at a considerably more advanced ontogenetic stage (see below). No denticulations of the keel are noticeable in this stage. (Specimen A.M.N.H. No. 25926:1, pl. 18, figs. 4–6.)

In the next stage, viz., between the diameters of 30 mm. and 70 mm., the costation becomes gradually more pronounced, and the ornamentation on the whole more regular. The ribs, 35 per half whorl, are now less prorsiradiate and assume a slightly sigmoidal course on the sides. Between every two primary ribs, one to three—quite exceptionally (anterior end of specimen A.M.N.H. No. 25926:2) even six—secondary ribs branch off the former or are plainly intercalated. Only the primary ribs carry distinct, radially elongated umbilical tubercles and equally distinct, though not very prominent, lateroventral ones. The latter are elongated, if at all, obliquely forward. The external ends of all the ribs, as visible on the venter, are uniform in strength. In specimens A.M.N.H. Nos. 25926:2 and 25926:3 a fine serration of the keel is just indicated on the cast; there seem to be about as many denticulations as ribs. This serration of the keel can be recognized much more distinctly on the penultimate whorl of specimen A.M.N.H. No. 25926:5 at diameters from 40 mm. to 65 mm. (pl. 18, fig. 3). Here 23 denticulations can be counted per half whorl. This is a little less than the total of both primary and secondary ribs and rather amounts to twice the number of primary ones. In side view these denticulations appear first triangular, with semicircular notches between them, then broad-trapezoidal, and somewhat wider than the notches separating them from one another.

The trend toward increasing regularity of ornamentation, mentioned above, persists in the next stage, studied in specimen A.M.N.H. No. 25926:4 at diameters from 70 mm. to 135 mm. (pl. 19, figs. 8, 9). Thirty-five ribs can still be counted per half whorl. Losing the slight sinuosity acquired in the preceding stage, they become straight again on the sides, and almost radial in direction. They are strong though not sharp, at least on the cast, and trend toward more uniformity. The secondary ribs, from two to five of which can be counted between two primary ribs, also extend to the umbilical edge or nearly so, and are hardly weaker than the primary ribs. The latter stand out chiefly by carrying strong circumumbilical nodes and less prominent, rather blunt, external ones. The inner nodes are elongated radially, the outer ones spirally or obliquely spirally. However, indications of external tubercles may also be found on some secondary ribs.

About the same general character of ornamentation as in the example just discussed is shown also by a corroded specimen of about the same size (A.M.N.H. No. 25927:1), which is, however, remarkable for exhibiting, at diameters from 90 to 100 mm., the nodes of the outermost row. Here, too, they are narrow and elongated in a spiral sense.

The latest stage of ornamentation in the typical form was studied on the outer whorl of the largest disk present (U.S.N.M. No. 103677, pl. 20, figs. 1, 2). Whereas the last quarter of the penultimate whorl, visible at least in part, exhibits still the costation of the last stage discussed, the secondary ribs disappear rather suddenly at the beginning of the outer volution. On this whorl there are only 22 ribs. The intercostals gradually increase orad in width. All the ribs are uniform. They begin indistinctly on or slightly below the umbilical shoulder and run in a straight and radial or slightly prorsiradiate direction across the sides. Then they cross the lateroventral edge at an angle of about 45 degrees, swelling to distinct but not very prominent horns, and continue on the venter, gradually vanishing toward the keel. No trace of the outermost row of the external twin nodes remains, but, preservation permitting, very slight undulations of the keel can be seen, from one to two of them corresponding to one rib. They are, undoubtedly, all that is

left of the former denticulations. Only a few ribs at about the second third of this volution show slight indications of circumumbilical tubercles. It may be worth noting that no change in the character of ornamentation can be noticed at the beginning of the body chamber in this specimen, whereas in the poorly preserved outer whorl A.M.N.H. No. 25927:1, measuring only about 150 mm. in diameter, a remarkable coarsening and a certain degeneration of the ornamentation set in on the body chamber, along with a considerable egression of the spiral of involution. Both these phenomena are frequently observed in Mesozoic ammonites.

(B) Var. **elegans**

The innermost one and a half whorls, well observable in paratype A.M.N.H. No. 25503: 1 (pl. 19, fig. 2) of this variety, appear to be smooth, or nearly so. Very soon afterwards, however, ornamentation sets in in the form of indistinct undulations on the sides. At a diameter of less than 2 mm. a distinct costation is clearly seen, and between the diameters of 3.5 mm. and 9 mm. 44 ribs can be counted on one whorl. They are very closely set, leaving but narrow intercostals between them, slightly sigmoidal, and, as a rule, are a little prorsiradiate. Even in this early stage primary and secondary ribs can readily be distinguished. From two to four of the latter may be counted between two of the former. However, all of them still originate independently at the umbilical shoulder. The primary ribs swell in their inner parts, thus indicating circumumbilical tubercles. The latter have moved closer to the umbilical shoulder and are more pronounced, though still decidedly elongated radially, at a diameter of a little less than 10 mm. Simultaneously bifurcation or trifurcation of primary ribs occurs at these inner tubercles. On the venter the ribs turn sharply forward and become particularly fine and uniform. Lateroventral nodes can first be observed, in specimens A.M.N.H. Nos. 25503:2 and 25503:3 (pl. 19, fig. 3), at diameters of about 15 mm. At this size they are still delicate, but they grow much stronger within half a volution and are, at least in some individuals (e.g., A.M.N.H. No. 25503:1, pl. 19, figs. 1, 2), quite pronounced at diameters between 20 mm. and 25 mm. They are elongated in a spiral or obliquely spiral sense. As a rule they are found on primary ribs only. Frequently secondary ribs, which branch off a primary one at the circumumbilical tubercle, unite again with the same in the external node. Occasionally (A.M.N.H. No. 25503:1, pl. 19, fig. 2) both ribs even amalgamate, thus giving rise to extraordinarily broad costae crossing the whole of the sides. The same individual is also distinguished by exhibiting, at a diameter of about 17 mm., slight indications of the outermost nodes on the venter which, however, disappear again very soon.

The character of ornamentation remains about the same up to diameters of from 25 mm. to 35 mm., except that the ribs become more sigmoidal in some examples, e.g., in the topotype, Col. Univ. No. 10630a, in which the costation assumes a decidedly harpoceratoid aspect (pl. 19, fig. 5). However, the most characteristic feature of this stage is the extreme gracefulness and density of the costation, the latter being best illustrated by the total of ribs per whorl. It amounts in six specimens examined to from 65 to 80, and even in specimen A.M.N.H. No. 25503:1 (pl. 19, fig. 2), with the least dense costation within the present material, still to about 50, as in Whitfield's (1880, pl. 14, fig. 1) holotype, as compared to from 30 to 35 in specimens of the same size referred to the typical form of this species. From a diameter of about 15 mm. the costae can be seen to begin at the umbilical seam, whence they rise up the umbilical wall in a rursiradiate direction, and then to turn gently forward on the umbilical shoulder.

The fine and dense serration of the keel can be observed only where the test is preserved, viz., in the topotype, Col. Univ. No. 10630a, at a diameter of 17 mm. (pl. 19, fig. 4), then in the same specimen and in A.M.N.H. No. 25503:1 at diameters of 25 mm. and 30 mm., respectively. Under the magnifying glass the denticulations can be recognized as rounded-triangular in shape and separated from one another by more or less semicircular notches. There are a few more denticulations than ribs.

The next stage of ornamentation, between the diameters of 30 mm. and about 90 mm., differs from the preceding chiefly by the

fact that the costae become more uniform. The primary ribs stand out merely by thick, rursiradially elongated circumumbilical nodes and spirally or obliquely spirally elongated external ones; the latter, however, become gradually less prominent. Furthermore, the costae in this stage about equal the intercostals in width. Seventy ribs, rarely only 60, can be counted per whorl. (Specimens A.M.N.H. Nos. 25503:4, 25503:5, and 25912: 4, pl. 19, fig. 11, pl. 22, figs. 1, 2, pl. 21, figs. 2, 3.) The largest paratype (S.D.S.S.M. No. 1507, pl. 21, figs. 1, 5) stands out by its particularly dense ornamentation (almost 85 ribs on the last whorl) and by the fact that differentiation between primary and secondary ribs, the latter being restricted to the outer half of the sides, persists up to the anterior end.

Except in specimen A.M.N.H. No. 25503:1 mentioned above, external twin nodes could not be observed at any stage in this variety.

(C) Var. robusta

In this variety the ornamentation could be studied from a diameter of about 30 mm. on. Even in this comparatively early stage it is characterized by stout, blunt, radial, and straight primary ribs which carry strong, more or less circular tubercles on both the umbilical and lateroventral shoulders. Sometimes one primary rib immediately follows another; more often, however, from one to two secondary ribs are intercalated between them. Some secondary ribs cling to a primary one, branching off at the umbilical tubercle and rejoining it at the lateroventral one. In this stage (diameters between 30 mm. and 70 mm.) there are from 30 to 35 ribs per whorl. In this variety, too, they rise in a rursiradiate direction up the umbilical wall and turn gently forward while crossing the umbilical edge. After crossing the lateroventral one, they turn sharply forward and continue on the venter, where all become equally strong, almost as far as the keel. An outermost row of nodes is but feebly indicated in this stage. Its earliest occurrence is observed in specimen A.M.N.H. No. 25928:1 at a diameter of about 50 mm. (pl. 20, fig. 6), but soon they disappear again. Here they correspond in site to the lateroventral nodes and are linear and elongated in a strictly spiral sense. Similar nodes can be recognized, though less distinctly, in specimen A.M.N.H. No. 9528/1. Serration of the keel is but slightly indicated on the cast near the anterior end of the former individual.

In the next stage, corresponding to diameters from 70 mm. to 105 mm., the ornamentation of this variety remains about the same, except that the ventral nodes become more pronounced, less linear, and gradually change from a spiral elongation to an obliquely spiral one. Serration of the keel is easily recognizable at the beginning of the outer whorl of the holotype (pl. 22, fig. 3). In the cast seven low, rounded denticulations at this point correspond to four consecutive ribs.

In the last ontogenetic stage examined in this variety, reaching up to a diameter of 185 mm., the costation tends to become much more dense (attaining a total of about 35 ribs in the anterior half of the holotype) and less stiff, some of the costae assuming a sinuous course. Also the difference between primary and secondary ribs becomes less marked. Some umbilical tubercles are still very prominent, but the lateroventral ones decrease in strength, as do those of the outermost row (specimens A.M.N.H. Nos. 9528/1, 25928:2, pl. 23, fig. 2, pl. 22, figs. 3–5). All these changes, except the first, seem to be due chiefly to the degeneration of the ornamentation on the body chamber. In the fragment A.M.N.H. No. 9528/3 (pl. 21, fig. 6), which is septate throughout, the ribs are, on the contrary, clear cut and comparatively sharp. Almost regularly two secondary ribs are intercalated between two primary ones, and all form a flat, orad concave arc across the sides. Both umbilical and lateroventral tubercles remain prominent and sharp up to the anterior end of this fragment. The outermost ones, however, although still pronounced in its posterior half (pl. 21, fig. 4), tend to vanish toward the anterior end. Where the high keel is preserved with the test it shows a minute serration, five denticulations corresponding to three ribs.

(D) Incertae sedis

The ornamentation of the large fragment U.S.N.M. No. 103676 resembles to a certain degree that of the largest typical specimen (U.S.N.M. No. 103677), but it still shows blunt inner tubercles, which have been shifted somewhat ventrad from the umbilical shoulder, and much more pronounced outer horns (pl. 24, figs. 2, 3).

In the other large whorl fragment, A.M. N.H. No. 25469, the costation is in general character very similar to that of the largest typical specimen, but the intercostals are almost twice as wide (pl. 23, fig. 3, anterior fragment).

As in the largest representatives of the *forma typica*, no traces of the nodes of the outermost row are found in the two large fragments here discussed, but the same very slight undulations of the keel, reminiscent of its serration in earlier ontogenetic stages, are recognizable, quite distinctly in specimen U.S.N.M. No. 103676, less so in specimen A.M.N.H. No. 25469. In both from two to three of these undulations seem to correspond to a rib and the following intercostal.

SUTURE LINES

(A) Forma typica

The earliest suture lines that could be properly studied were found in specimen A.M.N.H. No. 25926:1 at diameters from 17.5 to 35 mm. At the former diameter (fig. 93) there is a moderately deep siphonal lobe whose terminal points coincide in position with the shallow furrows accompanying the keel. They diverge but little and are separated by a rather low, rounded, median knob. The external saddles are broad, occupying beyond the ventrolateral shoulders the outer third of the flanks. They are divided by a three-pronged lobule into two stems, the outer of which is far wider, but only slightly higher than the inner. The first lateral lobe is a little less deep than the siphonal one and wide. It ends in three rather blunt points, the middle of which is the largest and subdivided by a low, triangular leaflet, thus foreshadowing later developments (below and p. 210). The first lateral saddle is only slightly lower but markedly less wide than the external one and is also intersected by a short, three-pronged lobule. Of its two stems the inner is broader and slightly higher than the outer and subdivided by a secondary lobule. The second lateral lobe points decidedly ventrad. It attains only about a third of the depth of the first and is considerably narrower. It has two blunt terminal points and a lateral one at its outer margin. There follow a rounded, bifid second lateral saddle, a short auxiliary lobe which rides just on the umbilical shoulder and seems to be three-pronged, and on the umbilical wall an auxiliary saddle with the beginning of another lobe visible beyond it. Altogether this suture line is a rather simplified one, though not to the degree that would have been expected from White's (1880, pl. 15, fig. 1e) drawing, reproduced with slight improvements by Stanton (1893, pl. 40, fig. 4), which shows a suture line corresponding to a much larger size.

The next sutural stage was studied in specimen A.M.N.H. No. 25926:4 at diameters from 70 to 110 mm. (fig. 95). The broad, only little indented saddles are still the most characteristic features, but the terminal points of the lobes have become markedly longer and more pointed. These changes may account for the less simplified aspect of these suture lines, as compared to those of the earlier stage. The following changes in the mutual proportions of the main elements are worth noting. The first lateral saddle now decidedly overtops the external one. It is divided into three leaves, the middle of which is the highest and the inner the smallest. The difference in depth between the two lateral lobes has increased, the second attaining hardly a third of the length of the first. The first lateral lobe is still symmetrically trifid. Its middle branch is subdivided into two points, the inner of which is somewhat stronger and longer than the outer; the former is three-pronged, the latter two-pronged. These two terminal points are not now so much smaller than the adjacent lateral branches, thus indicating one of the ways in which these lobes change from trifid to bifid (above and p. 210). The second lateral lobe now points dorsad. Viewed along its axis it appears bifid. There is, however, a strong lateral point on its outer margin which makes this lobe appear trifid if its obliqueness is not

taken into account. Considering the clear cut points of both lateral lobes in this suture line one wonders whether the coarsened and extremely simplified aspect of White's and Stanton's drawings, quoted above, which are taken from about the same growth stage (see White's explanation of his pl. 15, fig. 1e), is not due merely to poor preservation.

So far as the visible parts of the suture line, viz., the first lateral lobe and the margins of the adjacent saddles, are concerned, about the same sutural characters are found, at diameters between 110 and 125 mm., in the smaller one of the two fragments which are listed as U.S.N.M. No. 103676.

The sutural development appears, however, to be further advanced in specimen A.M.N.H. No. 25927:1, although the diameter (about 110 mm.) is hardly greater than in A.M.N.H. No. 25926:4 and rather smaller than in the fragment just discussed. The proximity of the last septum may account for this acceleration of development, as it does for the fact that the septa are here much more crowded, thus causing the lobes to appear broader in proportion to the saddles. Measurement, however, proves this proportion to be essentially the same in all individuals examined. The distinctive feature of this suture seems to be the fact that the triangular leaflet intersecting the middle point of the first lateral lobe has grown to such an extent that the points separated by it must now be considered independent terminal points rather than prongs of the middle point, and the lobe itself, in consequence, bifid rather than trifid. This process has been seen to be foreshadowed at earlier stages (see p. 209). The other two terminal points have moved up the lateral margins of the lobe and decreased in size, thus relegating themselves to the rank of lateral points; the outer is considerably longer than the inner. The second lateral lobe no longer points dorsad and clearly shows two terminal points with one more point on either side, the outer of these lateral points being longer than the inner. The following elements of this suture line will be discussed below.

The same character of the first lateral lobe as in the suture just described is recognized in the last quarter of the penultimate volution, and in the first of the outer one, of the largest disk present (U.S.N.M. No. 103677) at diameters of about 110 and 140 mm. (fig. 97). In the latest stage studied in this specimen, between the diameters of 190 mm. (fig. 96) and 230 mm., the first lateral lobe still shows two strong terminal points separated by a triangular leaf and two lateral ones immediately above them. The latter are now more or less symmetrically arranged.[1] It will be noted that the pattern of this lobe is much less complex in this species than in individuals of *Prionotropis woollgari* of an even smaller size (cf., e.g., figs. 45, 91). In the suture line under discussion the outer main stem of the external saddle is still considerably broader, but only slightly higher, than the inner. Both are separated by a stout, trifid lobule with a blunt, clearly two-pronged middle point, and end in three leaves each. The first lateral saddle markedly overtops the external one and ends in two leaves only, the inner of which is higher than the outer. The second lateral lobe is only about half as deep as the first, rather wide, and ends in three rather blunt, two- or three-pronged points. The second lateral saddle is deeply intersected on its outer margin by a slender, three-pronged lobule and on its top by a much shorter one. There follow on the umbilical wall a short, bifid auxiliary lobe, an auxiliary saddle, another short lobe, another auxiliary saddle, and the outer half of the deep lobe preceding the internal saddle.

The internal suture line could be studied in specimen A.M.N.H. No. 25926:5 at a diameter of about 90 mm. (fig. 94). The antisiphonal lobe is trifid with an asymmetrically three-pronged middle point. Its lateral branches deeply intersect the adjacent internal saddles which are tall and rather slender. Toward the umbilical seam there follows a lobe as deep as the antisiphonal one and asymmetrically trifid. Its middle and inner points are three-pronged; the somewhat stunted outer one is two-pronged. There follow a low saddle, just riding on the umbilical seam, a short, bifid, second auxiliary lobe, a deeply bifid auxiliary saddle, and the clearly trifid first auxiliary lobe. In specimen A.M.

[1] This applies, however, only to the upper first lateral lobe shown in figure 96. The lower one shows the outer lateral point in a considerably higher position than the inner.

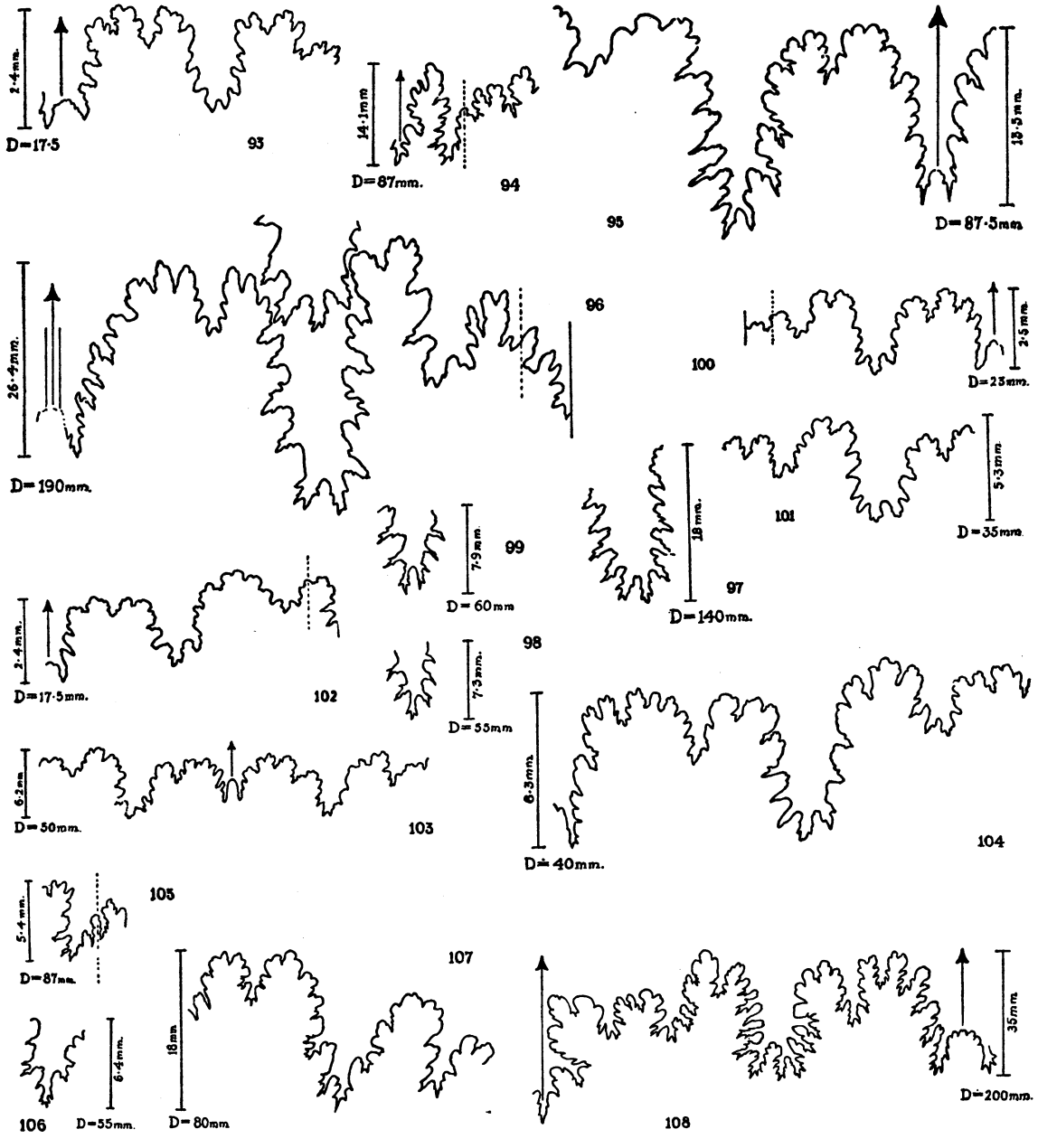
N.H. No. 25927:1, however, whose external suture has been discussed above, this lobe seems to have been reduced to a mere three-pronged lobule intersecting a broad amalgamated saddle, which seems to fill almost the whole width of the umbilical wall. The second auxiliary lobe seems to be even more reduced to another quite insignificant lobule of this amalgamated saddle. It cannot, however, reliably be decided whether or not this aspect is due merely to poor preservation.

The internal suture described above does not quite agree with the diagnosis given by Hyatt (1900, p. 589) for those of discoidal Prionotropidae in general: "reduced . . . to one pair of large saddles and one of incomplete lobes on either side of the antisiphonal," insofar as the lobes shown in figure 94 can hardly be called incomplete. Roman (1938, p. 455), thoroughly misunderstanding Hyatt's above diagnosis and translating it only in part, conveys the misleading impression that Hyatt meant all sutural elements, whereas he had only the internal ones in mind.

(B) Var. elegans

No illustration and virtually no description of the suture lines of this variety can be found in previous literature. Whitfield's (1880, p. 441) words "Septa rather simple . . . " hardly deserve to be called a description. Within the present material the earliest stage allowing a detailed study of the sutures corresponds to diameters between 10 and 20 mm. (A.M.N.H. No. 25503:1, fig. 102). The moderately wide siphonal lobe ends in two perpendicular points and has two more main points on either side. The median knob is low and rounded-trapezoidal in shape, with two slight notches on the top. The markedly broad external saddle is divided by a short, blunt lobule into two stems of the same height and about the same width. Both are subdivided by still shorter secondary lobules. The first lateral lobe is considerably shorter that the siphonal one. It is trifid, with a three-pronged middle point. Of the two other terminal points the inner is stronger than the outer up to a diameter of about 12 mm. The first lateral saddle is markedly higher but a little less broad than the external one, and is also divided by a short and blunt, dorsad oblique lobule. Of its two stems the inner is broader and higher than the outer. The second lateral lobe is very wide and shallow, hardly attaining half the depth of the first. At a diameter of 17.5 mm. it is clearly and almost symmetrically trifid. However, still within the stage here dealt with the inner point tends to exceed the outer one in length, and the latter is gradually shifted up the margin of this lobe, a process apparently preparatory to transition to bifidity (see p. 213). Simultaneously the difference in length between the inner and outer terminal points of the first lateral lobe begins to disappear. The second lateral saddle is lower than the first and trapezoidal in shape. It shows a slight middle notch. The greater part of it is on the umbilical wall. This saddle is followed by only one, rather deep, distinctly bifid auxiliary lobe whose inner margin is beyond the umbilical seam. Altogether the sutures are still very simplified in this early stage.

The next, between the diameters of about 20 and about 40 mm., could best be studied in topotype Col. Univ. No. 10630a (figs. 100, 101). The siphonal lobe is less wide than in the preceding stage, and the median knob taller. The lobule intersecting the external saddle has somewhat increased in depth and can be recognized as being three-pronged. The outer stem of this saddle shows now two secondary lobules instead of one, whereas the lobule of the inner stem has been shifted toward its inner margin. The first lateral lobe about equals the siphonal one in depth. At a diameter of about 23 mm. this lobe is still distinctly trifid. Of its three terminal points the outer has surpassed the inner in size and tends to become parallel and equal to the middle point which is still two-pronged. Only half a whorl later, at a diameter of 35 mm., both the middle and the outer points have become clearly three-pronged. These two points are now almost equal, whereas the difference in size between the outer and the inner one has still increased. However, if the disk is properly oriented, this lobe might still be considered trifid. The first lateral saddle, still slightly higher but much less broad than the external one, is almost symmetrically intersected by a short, three-pronged lobule. The second lateral lobe, about half as deep as the first, is narrower than in the earlier stage and bifid, its inner point being wider



FIGS. 93–108. Suture lines of *Prionocyclus wyomingensis* Meek.

93–97. *Forma typica;* 93, A.M.N.H. No. 25926:1; 94, A.M.N.H. No. 25926:5, antisiphonal lobe with adjacent part of left suture line; 95, A.M.N.H. No. 25926:4; 96, 97, largest specimen on record, U.S.N.M. No. 103677, 97, right first lateral lobe.

98–104. Var. *elegans*, new name; 98, 99, A.M.N.H. No. 25503:5, to show development of (left) first lateral lobe; 100, 101, Col. Univ. No. 10630a; 102, A.M.N.H. No. 25503:1; 103, A.M.N.H. No. 25503:4, showing asymmetry; 104, Col. Univ. No. 10630b.

105–107. Var. *robusta*, new variety; 105, holotype, A.M.N.H. No. 25928:2, left second lateral lobe; 106, 107, paratype A.M.N.H. No. 9528/1, 106, left first lateral lobe, 107, part of right suture line.

108. *Prionocyclus* cf. *wyomingensis* Meek, A.M.N.H. No. 25469.

Scale and diameter of disk (D) indicated for each drawing.

and longer than the outer; both are distinctly two-pronged. The second lateral saddle is considerably lower than the first. There follow on the umbilical wall a three-pronged auxiliary lobe with a lateral prong on its inner margin and a rather broad, bifid auxiliary saddle.

A similar suture line, though with still decidedly trifid first and bifid second lateral lobes, is found in specimen Col. Univ. No. 10630b at a diameter of about 40 mm. (fig. 104).

Essentially the same sutural characters as in specimen Col. Univ. No. 10630a are found in specimen A.M.N.H. No. 25503:4 where they persist up to a diameter of 50 mm., at least on the left side of the conch. On the right the suture lines are quite different. Between the diameters of 30 and 50 mm. a third stem is added to the external saddle on its inner side. It is separated by a deep lobule from its main body and attains only about two-thirds of the height of the latter, but is about as broad as the outer stem of this saddle. This extraordinary sutural element markedly narrows the first lateral lobe which is almost symmetrically trifid with a two-pronged middle point and two more short terminal points on either side (fig. 103).

In specimen A.M.N.H. No. 25505:5 a further development can be studied between the diameters of 55 and 60 mm., within the short range of about an eighth of a whorl (figs. 98, 99). At the former diameter (fig. 98) the first lateral lobe might still be called trifid, as in the preceding stage. At the latter (fig. 99), however, both outer and middle terminal points of this lobe are stretched in the spiral sense and are almost parallel to each other, but the middle one is still somewhat longer than the outer; the former is three-pronged, the latter two-pronged. Meanwhile the former inner terminal point, which is three-pronged, has moved up the margin of the lobe, simultaneously turning to an almost radial direction, so that it must now be considered a lateral point rather than a terminal one and the lobe itself bifid rather than trifid. Thus this case demonstrates a second way of transition of the first lateral lobe from trifidity to bifidity, different from that observed above (pp. 209, 210) in the typical form of this species, although repeatedly found (see pp. 181, 183, 189, 190) in various forms of *Prionotropis woollgari*. It is fascinating indeed to observe how the apparent ontogenetic aim of final bifidity of the first lateral lobe, as if predestined in the Prionotropidae, can be reached in two quite different ways. These observations cannot but suggest orthogenetic conceptions.

It seems noteworthy that bifidity of the first lateral lobe is achieved as early as at a diameter of 60 mm. in this variety but only at about 110 mm. in the *forma typica*. This seems to support the surmise stated above (p. 203) that this variety may have reached maturity at a smaller size than the typical form.

It may be added that in one of the two largest disks of this variety (A.M.N.H. No. 25912:4) the bifid stage of the first lateral lobe is also reached at a diameter of about 60 mm. However, the surface of this specimen is too corroded for an exact study of the sutural characters.

The next sutural stage of the variety *elegans* is observable in specimens A.M.N.H. Nos. 25912:2 and 25912:6 and S.D.S.S.M. No. 1507 at diameters of 68, 77, and 63 mm., respectively. In the first the difference in length between the two remaining terminal points of the first lateral lobe has decreased. In the two others it has disappeared so that this lobe is now unequivocally bifid with two equal terminal points, both of which can be recognized as being subdivided into two secondary points. Of the latter some seem to be three-pronged, some two-pronged.

(C) Var. robusta

Since the smallest individual representing this variety is too corroded for a study of sutural characters, the earliest stage permitting of any such observations is found in paratype A.M.N.H. No. 9528/1 at a diameter of 55 mm. Here (fig. 106) the first lateral lobe is seen to be trifid with a long middle branch which ends in a three-pronged middle point and two lateral ones, the inner of which occupies a higher position than the outer. Both lateral branches are subdivided into a stronger, three-pronged lower point and a shorter, two-pronged upper one. At a diameter of 80 mm. the right suture line is visible in the same specimen from the external

saddle to the second lateral one (fig. 107). The external saddle seems to be even wider than in other forms of this species and is almost symmetrically intersected by a comparatively deep, trifid lobule with a three-pronged middle point. The first lateral lobe points ventrad and has a strong middle branch which is deeply subdivided into a shorter, two-pronged outer point and a longer, three-pronged inner one. The lateral branches agree in pattern fairly well with those shown in figure 106, but they are so much less conspicuous than the bifid middle branch that this lobe must be called bifid rather than trifid. The first lateral saddle is much lower and less wide than the external one and is followed by a ventrad oblique, rather narrow, almost symmetrically bifid second lateral lobe with a two-pronged outer terminal point and a three-pronged inner one. In addition, there are two points on either side of this lobe which just rides on the umbilical shoulder.

In the holotype (A.M.N.H. No. 25928:2), the first lateral lobe can be recognized as being still trifid at a diameter of somewhat above 90 mm., but it is too poorly preserved for delineation. However, a second lateral lobe is excellently seen at a diameter of about 87 mm. (fig. 105). It is shifted even farther dorsad than in the suture described above, most of its width being beyond the umbilical edge. This dorsad shift is obviously due to the stoutness of the whorl. If judged by its middle axis, this second lateral lobe can be seen to point dorsad and must then be considered bifid (cf. the typical form between the diameters of 70 and 110 mm., pp. 209–210) with a longer and broader, bifid outer point and a much shorter and sharper inner one. In addition, there are two lateral points, the outer of which is by far the longer. Dorsad there follows a high, comparatively richly indented second lateral saddle.

Summarizing, this variety also exhibits the trend toward bifidity of the first lateral lobe in maturity, but this ontogenetic aim is achieved in one specimen (A.M.N.H. No. 9528/1) only, shortly before the last septum, at the comparatively great diameter of 80 mm. Thus the sutural development of this variety may be considered slower than in the other forms of this species.

(D) **Incertae sedis**

In the large fragment U.S.N.M. No. 103676 (the sutures of the smaller fragment comprised in this catalogue number have been mentioned above, p. 210) sutures could be studied between the diameters of 220 and 250 mm. They differ from the same stage of the typical form, as studied in U.S.N.M. No. 103677 (see p. 210, figs. 96, 97), in some respects. The siphonal lobe is somewhat narrower and the median knob taller and more slender. The external saddle is extremely broad, more so than in U.S.N.M. No. 103677. This is particularly true of its outer main stem; the difference in width between both main stems is, therefore, more pronounced; also the outer is rather deeply intersected by a three-pronged secondary lobule. The first lateral lobe, only a little deeper than the siphonal one, appears to be narrower than in the typical form, and the triangular leaf separating its two terminal branches is taller and more slender. The first lateral saddle about equals the external one in height. The second lateral lobe is distinctly trifid, as in the *forma typica*, but less wide. There follow, from the umbilical shoulder dorsad, a broad, rectangular, bifid second lateral saddle, a rather shallow, distinctly bifid auxiliary lobe, and a small, rounded, simple auxiliary saddle whose inner margin is just on the umbilical seam. The internal suture line could not be made visible.

From this suture, that of the fragment A.M.N.H.No. 25469, previously (Haas, 1943) misidentified as "*Pervinquieria* cf. *romeri*," which is entirely preserved at a diameter of somewhat above 200 mm. (fig. 108), deviates only in some details. The siphonal lobe is wider, as is the median knob. At the bottom of the first lateral lobe there are two more triangular leaves on both sides of the middle one which is in turn lower and altogether smaller than in U.S.N.M. No. 103676. The second lateral lobe points slightly dorsad, and the auxiliary one has immediately above its two terminal points, the outer of which is the stronger and two-pronged, two lateral, unequally two-pronged points. The second auxiliary lobe, observed in the typical form (specimens A.M.N.H. No. 25926:5 and U.S.N.M. No. 103677, see figs. 94 and 96), seems to be reduced to a small, three-pronged

lobule of the sturdy, dorsad-inclined internal saddle, and the narrow deep lobe on the outer side of that saddle, still well seen in both figures cited, has entirely disappeared, as it has in the later stages of *Prionotropis woollgari* (cf. p. 185, fig. 45). The antisiphonal lobe shows a strong, trifid median branch, with a slender, three-pronged middle point and a bifid lateral branch on either side, with a stronger and three-pronged lower point and a weaker and two-pronged upper one. In addition, there are minor indentations along the inner margin of the internal saddle, the uppermost of which might be called another lobule of this saddle.

MATERIAL STUDIED; ITS RANGE AND DISTRIBUTION

(A) *Prionocyclus wyomingensis* Meek, *forma typica*

A.M.N.H. No. 9529/1: A specimen from "below black shale of Ft. Pierre," probably Benton shale, 10 miles south of Edgemont, South Dakota; collector, Barnum Brown, 1903.

A.M.N.H. No. 25926: Five specimens from the same horizon, 10 miles southwest of Edgemont, South Dakota; collector, Barnum Brown, 1903.

A.M.N.H. No. 25927: Two specimens, probably from Benton shale, locality unknown; collector, F. B. Loomis, 1902.

U.S.N.M. No. 103677: A large disk from the upper part of the Carlile shale, near Rocky Point, Campbell County, Wyoming; collectors, Hoots and Rubey, 1923.

(B) *Prionocyclus wyomingensis* Meek, var. *elegans*, new name

A.M.N.H. No. 25503: Eight specimens from the top of the Carlile shale, *ca.* 5 miles west of Newcastle, Wyoming (on side of highway to Lusk); collector, H. E. Vokes, 1936.

A.M.N.H. No. 25912: Six specimens from "below black shale of Ft. Pierre," probably Benton shale, 10 miles southwest of Edgemont, South Dakota; collector, Barnum Brown, 1903.

A.M.N.H. No. 25912/1: A specimen from the same horizon, 10 miles south of Edgemont, South Dakota; collector, Barnum Brown, 1903.

Col. Univ. No. 10630: Three specimens from the Cretaceous, East Fork of Beaver Creek, Black Hills, Dakota (topotypes).

S.D.S.S.M. No. 1507: A medium-sized disk from second ridge above base, Carlile formation, 10 miles east of Hot Springs, South Dakota.

S.D.S.S.M. No. 1674: Two specimens from same horizon, same locality.

S.D.S.S.M. No. 1675: A half disk, horizon not known, from same locality.

(C) *Prionocyclus wyomingensis* Meek, var. *robusta*, new variety

A.M.N.H. No. 9528/1: A medium-sized disk (paratype), probably from Benton shale, locality unknown; collector, F. B. Loomis, 1902.

A.M.N.H. No. 25928: A small disk (No. 1, paratype) and a big disk (No. 2, holotype) from "below black shale of Ft. Pierre," probably Benton shale, 10 miles southwest of Edgemont, South Dakota; collector, Barnum Brown, 1903.

A.M.N.H. No. 9528/3: A fragment (paratype) from the Ft. Benton group, locality given as "6 miles from Ogden, Utah," though adding, "very uncertain"; collector, C. D. Gwyer.

(D) (a) *Prionocyclus wyomingensis* Meek?

U.S.N.M. No. 103676: Two fragments from the Mancos shale, Antonio Sedillo Grant, 18,000 feet south of north line and 7500 feet east of west line, near Suwannee, Valencia County, New Mexico; collector, H. R. Joesting for C. B. Hunt.

(b) *Prionocyclus* cf. *wyomingensis* Meek

A.M.N.H. No. 25469: A whorl fragment, probably from the Mancos shale, 2 miles south of Cebolletta, Valencia County, New Mexico; collector, George X. Frey, 1939.

TOTAL: Thirty-eight specimens.

As seen from the above list, the geographic range of this species almost coincides with that of *Prionotropis woollgari*. So far as precise horizon data are available, they indicate that this species occurs in the upper part of the Carlile shale, whereas *Prionotropis woollgari* seems to be restricted to its lower part (see p. 199), thus corroborating the well-known fact (cf. Muller and Schenck, 1943, p. 272, fig. 6; Moreman, 1942, p. 194) that *Prionо-*

cyclus occupies a somewhat higher site in the stratigraphic column of the Turonian of North America than *Prionotropis*. This fact, as applied to the type species of both these genera, *Prionocyclus wyomingensis* on the one hand, and *Prionotropis woollgari* on the other, becomes particularly clear in the geological cross section of the locality 10 miles east of Hot Springs, South Dakota, where, according to a field sketch kindly supplied by Prof. J. P. Gries, the latter species is found on the "first ridge" only, whereas the former has been collected solely from the "second ridge" which is, in that section, about 115 feet above the first.

Moreover, the above list shows that all three of the forms distinguished within this species, the typical one as well as the varieties *elegans* and *robusta*, were found associated with one another at the same locality (10 miles southwest of Edgemont, South Dakota), apparently in the same horizon. Therefore, they cannot be utilized for purposes of zonal differentiation.

VALID DIFFERENCES BETWEEN THE TWO SPECIES AND THEIR GENERIC SIGNIFICANCE

IN THE PRECEDING SECTIONS OF THIS REPORT the intraspecific variation within the polytypic species *Prionotropis woollgari* and *Prionocyclus wyomingensis* has been studied, and the ontogeny of each of the various forms of both these species has been closely followed. In conclusion, it might seem advisable to consider them as species units and to compare them as such with each other. Since both happen to be the type species of their genera, such comparison may well serve the purpose of finding out the distinctive generic characters of *Prionotropis* on the one hand and of *Prionocyclus* on the other.

Meek, when splitting off (1876, pp. 452–453) *Prionotropis* as a subgenus from his genus *Prionocyclus* established five years earlier (1871, p. 289, footnote 8), gave diagnoses of *Prionocyclus, sensu lato*, as well as of both its subgenera (or "sections," to use his own word) *Prionocyclus, sensu stricto*, and *Prionotropis*. The last two diagnoses were, however, based on the material available to him at that time and can hardly stand a critical examination on the strength of our present knowledge. For example, sharply defined costae in the adolescent stage (called "very young" by Meek) occur in the varieties *elegans* and *robusta* of *Prionocyclus* as well as in *Prionotropis woollgari*, but Meek, who at that time knew only typical specimens of both species under discussion, made this character a distinctive one of the subgenus *Prionotropis, sensu stricto*. Both species are, by the way, smooth in that growth stage that might justly be called very young. Moreover, secondary ribs, believed by Meek to be restricted to *Prionocyclus, sensu stricto*, and to be entirely missing in *Prionotropis*, occur, though not quite so regularly and only in certain ontogenetic phases, in *Prionotropis woollgari* as well, particularly in its varieties *regularis* and *praecox*. It is true that the keel is "not broken into a series of isolated, elongated nodes" in *Prionocyclus wyomingensis*, as it is in *Prionotropis woollgari*, but it is serrated all the same in the former species, a character not mentioned and perhaps overlooked by Meek, who calls its keel "continued prominent."

Adkins (1928, p. 249), however, clearly recognized that the keel furnishes a valuable distinctive character between *Prionocyclus* and *Prionotropis;* he states that it is "entire or very minutely serrate in adult" in the former genus, but "serrate or nodose in adult" in the latter. This distinction is certainly applicable to the type species of both these genera; however, it constitutes but one of several distinctive features. Others are provided by the ornamentation on the one hand and by the sutures on the other. The most obvious sculptural difference results from the dominance of the tubercles in the mature ontogenetic stages of *Prionotropis woollgari*, whereas they play only a minor part in *Prionocyclus wyomingensis*. However, even the external "twin nodes" so characteristic of the former species are recognizable in certain forms of the latter, particularly in its variety *robusta*,[1] in whose holotype and paratype A.M.N.H. No. 9528/3 they are found to persist even longer (up to diameters of about 150 and 180 mm., respectively) than in any examined specimen of *Prionotropis woollgari*. Nodes may be said to constitute the dominant sculptural elements at maturity even in the variety *praecox* of the latter species which otherwise most closely approaches *Prionocyclus wyomingensis*. Another sculptural character distinctive of *Prionocyclus wyomingensis* except, as must be emphasized, for its last ontogenetic stage is the differentiation between primary and secondary ribs, with nodes as a rule restricted to the former. As stated above, secondary ribs appear in certain forms of *Prionotropis woollgari* also, particularly in its varieties *regularis* and *praecox*, but with the only exception of the variety *praecox*, which also in this respect most resembles the younger species, they are confined to a comparatively short ontogenetic phase and they dis-

[1] They seem to be visible in White's (1880, pl. 14) figure 1b, but no mention of them is found in either his or Whitfield's (1880) descriptions.

appear altogether earlier. Moreover, there is as a rule only one secondary rib between two primary ones in *Prionotropis woollgari* (again excepting its variety *praecox*), whereas from two to five may often be counted in *Prionocyclus wyomingensis*.

As to sutural characters, the sutures of *Prionocyclus wyomingensis*, although this is the younger species, appear to be simplified as compared to those of *Prionotropis woollgari*, with sturdier, much less deeply intersected saddles and shorter and blunter points of the lobes. In this respect also the variety *praecox* of the latter species seems somewhat to approach the former. A particularly distinctive character is the median knob of the siphonal lobe which is always and in the later ontogenetic stages even richly indented in *Prionotropis woollgari*, but shows only occasionally slight indentations in *Prionocyclus wyomingensis*.

Can generic significance be assigned to all these differences? Since the species here compared are both genotypes, generic separation of *Prionotropis* and *Prionocyclus* cannot be justified unless the answer to the above question is in the affirmative.

In the writer's opinion it can be so only by the standards of modern ammonitological taxonomy which favors a narrow circumscription of genera. In Meek's days it was certainly more adequate to consider both groups, as he did (1876, p. 453), as "sections of one genus," viz., *Prionocyclus*. Should, therefore, only subgeneric rank be granted to the *woollgari* group, it would have to be treated again, as it was by Meek, as the subgenus *Prionotropis* of the genus *Prionocyclus*, *sensu lato*. However, it seems that hardly anything would be gained by such a procedure, since subgeneric names tend to eliminate and replace the generic ones as time goes by (cf. Haas, 1942c, p. 5). It is therefore my belief that the best thing to do is to maintain both *Prionotropis* and *Prionocyclus* as independent genera, though I am fully aware of their close relationship, as demonstrated best by the almost transitional character of the variety *praecox* of *Prionocyclus woollgari*. This decision is certainly favored by the fact that at least the type species of these genera are clearly separated stratigraphically (see pp. 215–216).[1]

[1] Furthermore, the above solution avoids the issue that would otherwise arise of whether or not Hyatt's (1900, p. 589) family name Prionotropidae need be replaced by Prionocyclidae.

HOMEOMORPHIES BETWEEN ALBIAN PERVINQUIERINAE AND CERTAIN UPPER CRETACEOUS PRIONOTROPIDAE

THE TERM "HOMEOMORPHY" used above presupposes lack of relationship or at least of direct relationship between the groups concerned. According to Spath (1926, p. 79) they are "somewhat homoeomorphous, but unrelated," and there is as yet no evidence to the contrary. Roman (1938, p. 461, table), on the other hand, derives both *Prionotropis* and *Prionocyclus*,[1] though doubtfully, from the Dipoloceratidae which, according to Roman (1938, pp. 367, 372) as well as Spath (1942, p. 705; cf. Haas, 1944a), include the Pervinquierinae (=Mortoniceratinae Spath, 1942).

If the law of recapitulation, so strongly questioned by Spath (for references, see Haas, 1942c, p. 143), may be relied upon, then the smoothness of the earliest ontogenetic stages of all the forms concerned might support the view that both Pervinquierinae and Prionotropidae arose, perhaps independently, from some smooth, pelagic "conservative stock." According to both Spath (1923, pp. 14, 32, 33; 1927, pp. 63, 64; 1933, p. 3; 1942, pp. 682–683) and Salfeld (1924) such "conservative stocks" gave rise again and again to sculptured stocks of neritic ammonites which, though unrelated, may more or less closely resemble each other.

The homeomorphy between some Albian forms of the genus *Pervinquieria* and certain Upper Cretaceous Prionotropidae of the genera *Prionotropis*, *Prionocyclus*, and *Texanites* may go very far indeed. It even includes such peculiar features as the change from a fine and dense costation in earlier ontogenetic stages to a robust one with rather wide intercostals in maturity, equally encountered in *Pervinquieria arietiformis* (Spath) (see Haas, 1942c, p. 90) on the one hand and *Prionotropis woollgari* and *Prionocyclus wyomingensis* on the other.

[1] Independently as collateral relatives, whereas both paleontological and stratigraphical evidence would suggest, for North America, derivation of *Prionocyclus* from *Prionotropis*. The variety *praecox* of *Prionotropis woollgari* might still prove to be not only morphologically but phylogenetically intermediate between the type species of these genera.

No wonder, then, these homeomorphies repeatedly misled students. The classical case, which has brought about so much taxonomic confusion,[2] is Gabb's identification, uncritically accepted by Meek (1876, p. 448, footnote), of *Ammonites vespertinus* Morton, an Albian pervinquierid (=mortoniceratid), with *Ammonites texanus* Roemer, later designated the genotype of the Senonian *Texanites* by Spath. Another example is my own (Haas, 1943) misidentification of a fragment of a *Prionocyclus* cf. *wyomingensis* from New Mexico as "*Pervinquieria* cf. *romeri*." It might be called an irony of fate that I myself, who some months earlier (Haas, 1942b) had emphasized the recurrence of morphologic types in Mesozoic ammonites, fell victim to one of the manifold fallacies of this very phenomenon. In this particular case, what made things worse is the fact that even the suture lines, yielding the most reliable distinctive characters in other cases of this kind (see below), proved to be of no avail. For the sutural differences between that fragment and the paratype of *Pervinquieria romeri*, pointed out in detail in the paper quoted above (Haas, 1943, pp. 1, 2), are hardly greater than those prevailing between different species of the genus *Pervinquieria*. To demonstrate the likeness between that fragment and the paratype of *Pervinquieria romeri* Haas, both are shown fitted together in ventral and side views on plate 23, figures 1 and 3.

One more case was fortunately discovered in time. Among the specimens of the American Museum of Natural History labeled "*Prionotropis woollgari*," there was a rather corroded disk, not so dissimilar from the specimen U.S.N.M. No. 103907a, referred above to the typical *Prionotropis woollgari*, or from the specimen Col. Univ. No. 15002, described and figured by Johnson (1903) and referred above to the variety *intermedia* of that species. From both it differs mainly by exhibiting bifurcation of ribs and differentiation between primary and secondary ribs,

[2] See Haas, 1942a, pages 10, 11; 1942c, pages 66, 67.

both persisting up to a diameter of about 140 mm., and a higher umbilical wall. However, taking into account the extreme variability of *Prionotropis woollgari*, these differences need not have suggested specific, not to say generic, separation, had not the lithological character of the matrix, not found in any other *Prionotropis* under examination, aroused suspicion. It led to the discovery that specimen and label did not belong together and that the former most probably comes from Medina River, Bandera County, Texas. Careful examination proved it to be an Albian *Pervinquieria*, viz., an adult individual of *P. wintoni* (Adkins).

These troubles of necessity raise the question as to whether there exist any reliable criteria for the distinction of Pervinquierinae from certain Prionotropidae, even where only fragments just exhibiting one ontogenetic stage are available. (Whenever the development can be studied, no such doubts are likely to arise.) In my experience, there is one distinctive character in ornamentation, and there are some in the suture lines. The former may be found in the fact that in the Prionotropidae the ribs, or growth striae replacing them in late ontogenetic stages, run in a decidedly rursiradiate direction across the umbilical wall and turn forward on the umbilical shoulder only, whereas this feature is not found in the Pervinquierinae. However, wherever the surface is corroded, this difference will be of no avail. Furthermore, the suture lines seem to be altogether less richly indented and, in particular, the saddles to be more sturdy and less deeply intersected by lobules in the Prionotropidae than in the Pervinquierinae, and the first lateral lobes are more pronouncedly bifid and altogether more symmetrical in the latter than in the former.

SUMMARY

EXAMINATION OF ABOUT 450 SPECIMENS of *Prionotropis woollgari* Meek (? *non* Mantell) and about 40 of *Prionocyclus wyomingensis* Meek from various localities in the western interior of the United States proves a high degree of both intraspecific variation and ontogenetic changes in these two ammonite species, often quoted and repeatedly used as index fossils but hardly ever thoroughly studied since their establishment. The interaction of both factors causes an almost bewildering diversity of morphologic aspects, particularly in *Prionotropis woollgari*. Both species are considered polytypic.

The original of Meek's (1876, pl. 7) figure 1a, b, is designated lectotype of the typical *Prionotropis woollgari* Meek. Six varieties: *crassa*, *intermedia*, *regularis*, *tenuicostata*, *praecox*, and *alata*, the last based on the individual figured by Meek (1876) on plate 6, figure 2, and plate 7, figure 1g, h, are separated from the typical form, with *P. branneri* Dickerson considered a seventh. In addition to *Ammonites percarinatus* Hall and Meek, *Ammonites graysonensis* Shumard is also included in the synonymy of Meek's species. The ontogeny of the *forma typica* as well as of the six new varieties is closely followed with respect to dimensions, length of body chamber and full size attained, whorl section, ornamentation, and sutures. This study shows that intraspecific variation is largely due to differentiation in speed of development. Particularly interesting are sculptural and sutural ontogenies, the former for the appearance, further development, vanishing, and eventual disappearance of the various elements of ornamentation and for its general trend toward diminishing fineness and density, the latter for the trend of the first lateral lobe to change from trifidity to bifidity (and frequently of the second lateral lobe to change simultaneously from bifidity to trifidity).

White's (1880) specimens of *Prionocyclus wyomingensis* are recognized as being typical of this species of Meek's. Two varieties, *elegans*, based on Whitfield (1880), and *robusta*, are separated from the typical form, and two large fragments belonging or closely related to this species are discussed as "*incertae sedis*." The ontogeny is studied along the same lines as in *Prionotropis woollgari*, with similar results, especially as to sutural development. It can be shown that the change of the first lateral lobe from trifidity to bifidity can be achieved in two different ways (orthogenesis?).

As both species are genotypes, the differences between them stand for those between their genera. These differences are discussed and found just sufficient to warrant—by the standards of present taxonomy—generic separation. The variety *praecox* of *Prionotropis woollgari*, however, is somewhat transitional between both genera.

Homeomorphies between Albian Pervinquierinae and certain Upper Cretaceous Prionotropidae are exposed and illustrated by several examples, and an attempt is made to point out some sculptural and sutural differences between both groups.

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[1] Incorrectly printed; see title of this paper.

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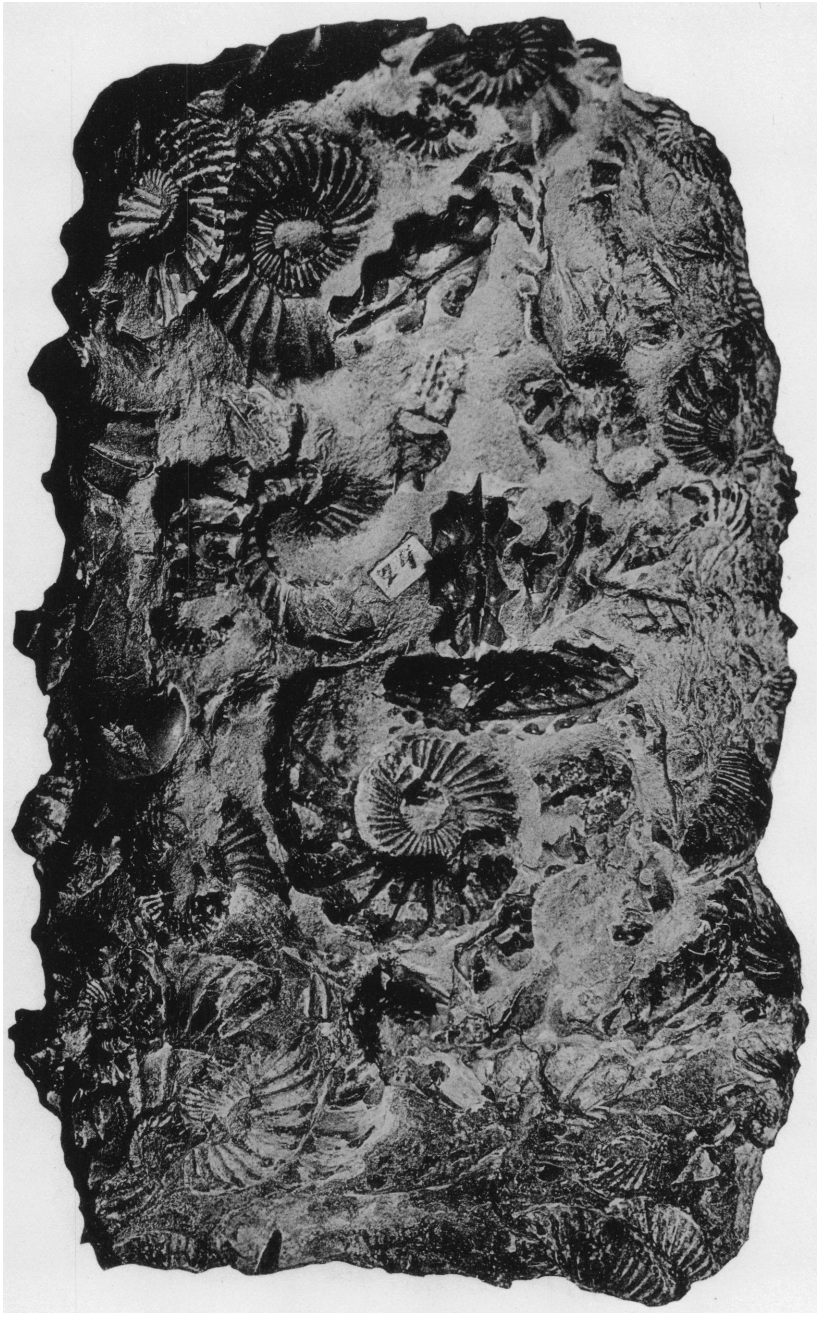
PLATES 11–24

PLATE 11

The "unnumbered block" of the United States National Museum, crowded with shells referable to various forms of *Prionotropis woollgari* Meek (? *non* Mantell), *sensu lato*, before preparation; probably collected by the Powell Survey in southern Utah, exact locality unknown; natural size. Compare plate 12 and plate 24, figure 1.



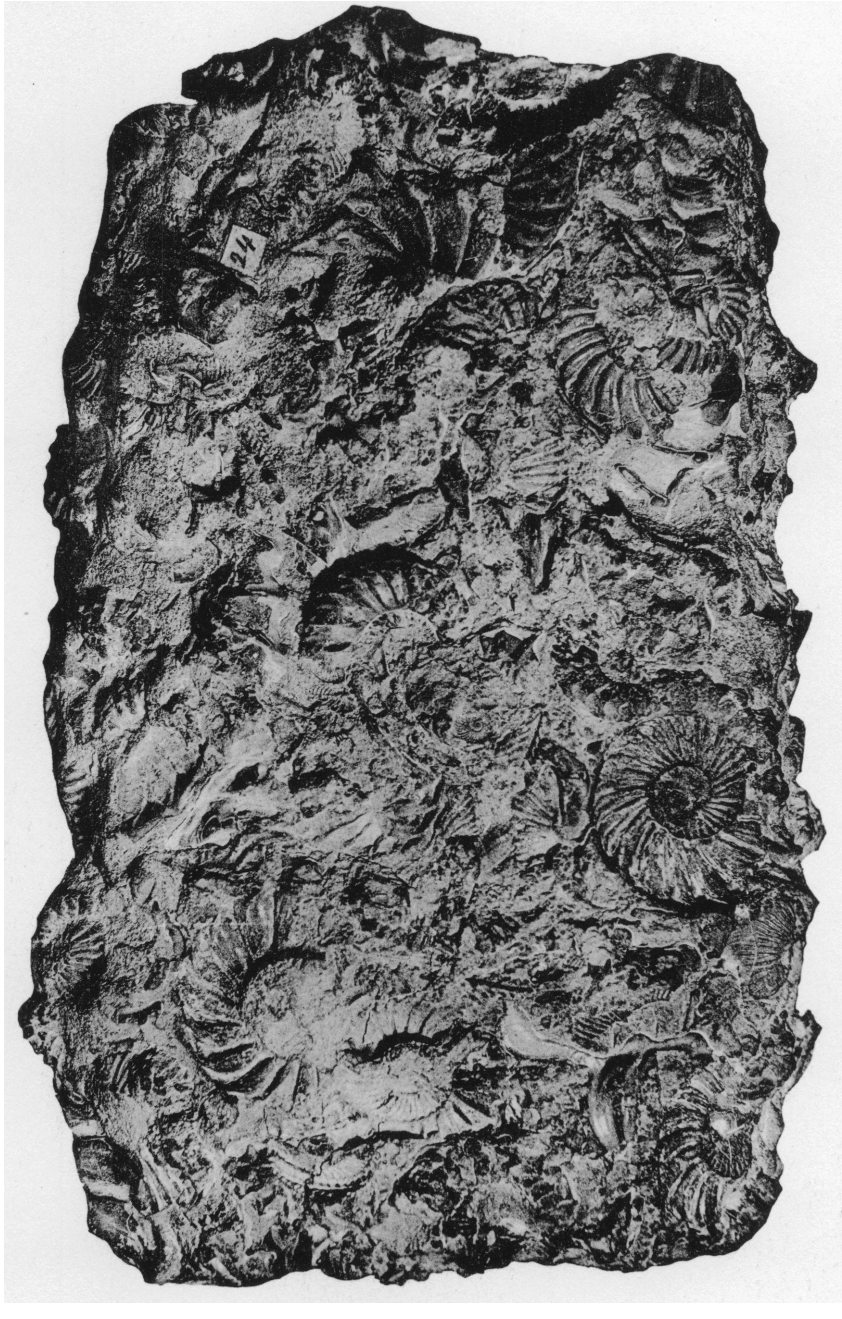

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PLATE 12

The "unnumbered block" of the United States National Museum from reverse side of that on plate 11; natural size. Compare plate 11 and plate 24, figure 1.

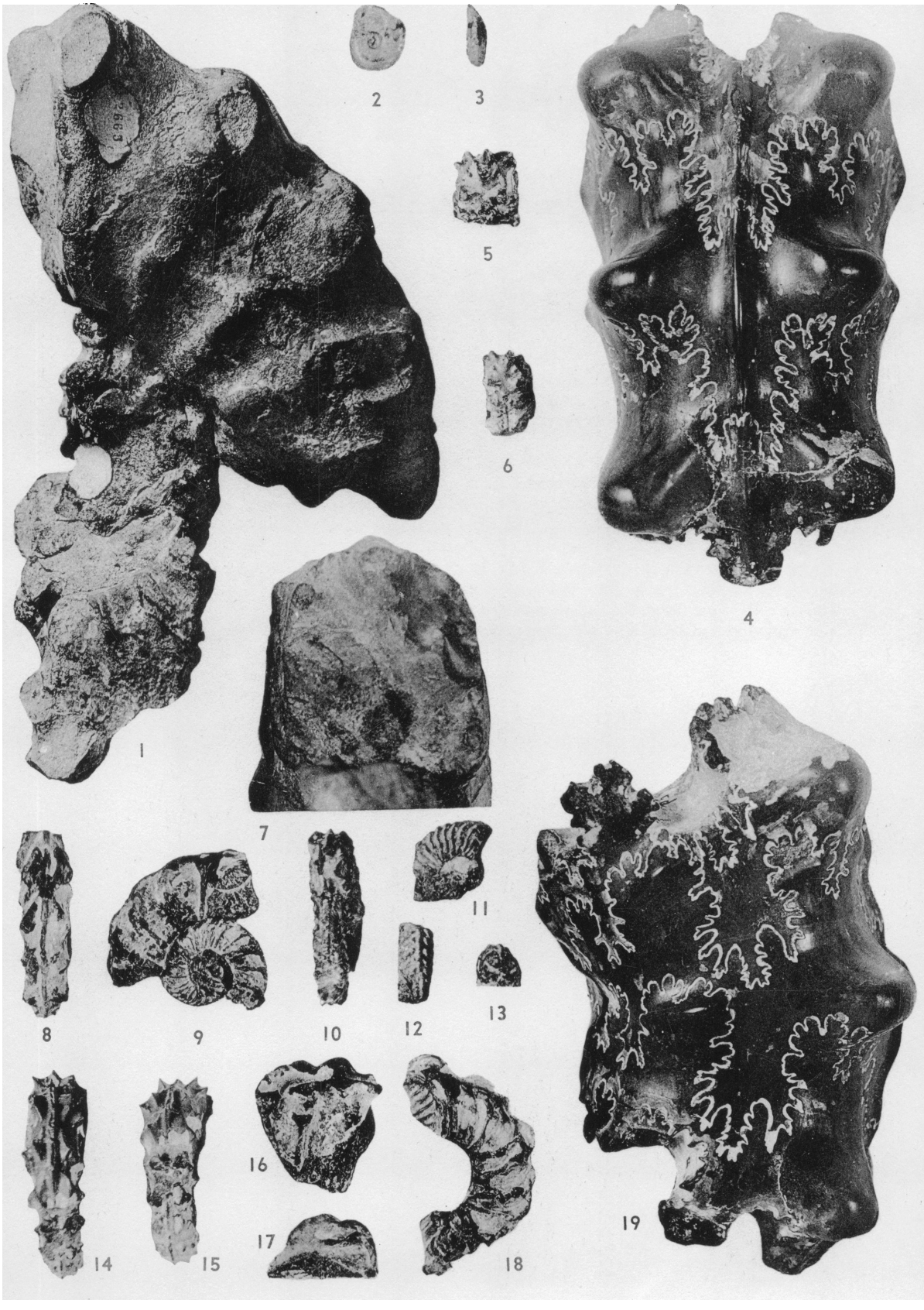
PLATE 13

1, 4–19. *Prionotropis woollgari* Meek (? *non* Mantell), *forma typica*. 1, 7. U.S.N.M. No. 103907a; 1, left side view; 7, section at posterior end of preserved part of outer whorl. 4, 19. C.N.H.M. No. P5932; 4, ventral view; 19, left side view. 5, U.S.N.M. No. 103895j; section at posterior end. 6, U.S.N.M. No. 103895i; section at posterior end of anterior fragment. 8–10, U.S.N.M. No. 103895e; 8, ventral view; 9, right side view; 10, sectional view at fracture. 11–13, U.S.N.M. No. 103895m; 11, right side view, 12, ventral view, 13, section at anterior end, of inner nucleus; all ×2. 14, 15, U.S.N.M. No. 103895h; 14, ventral view; 15, another ventral view, slightly oblique, to show three-pronged aspect of periphery. 16, U.S.N.M. No. 103895o; right side view of a whorl fragment, to show details of cockscomb keel. 17, U.S.N.M. No. 103895p; left side view of a fragment, to show a single tooth of cockscomb keel, with orad slope much steeper than apicad one. 18, U.S.N.M. No. 103895n; left side view of a half whorl with, anteriorly, well-developed cockscomb keel.

2, 3. *Prionotropis woollgari* Meek (? *non* Mantell). A disk too small to be assigned to any given form within this species, U.S.N.M. No. 103900a; 2, left side view; 3, ventral view; both ×2; to show beginning of ornamentation and keel.

Unless otherwise indicated, all figures are natural size.

For horizons and localities, see pages 197–199.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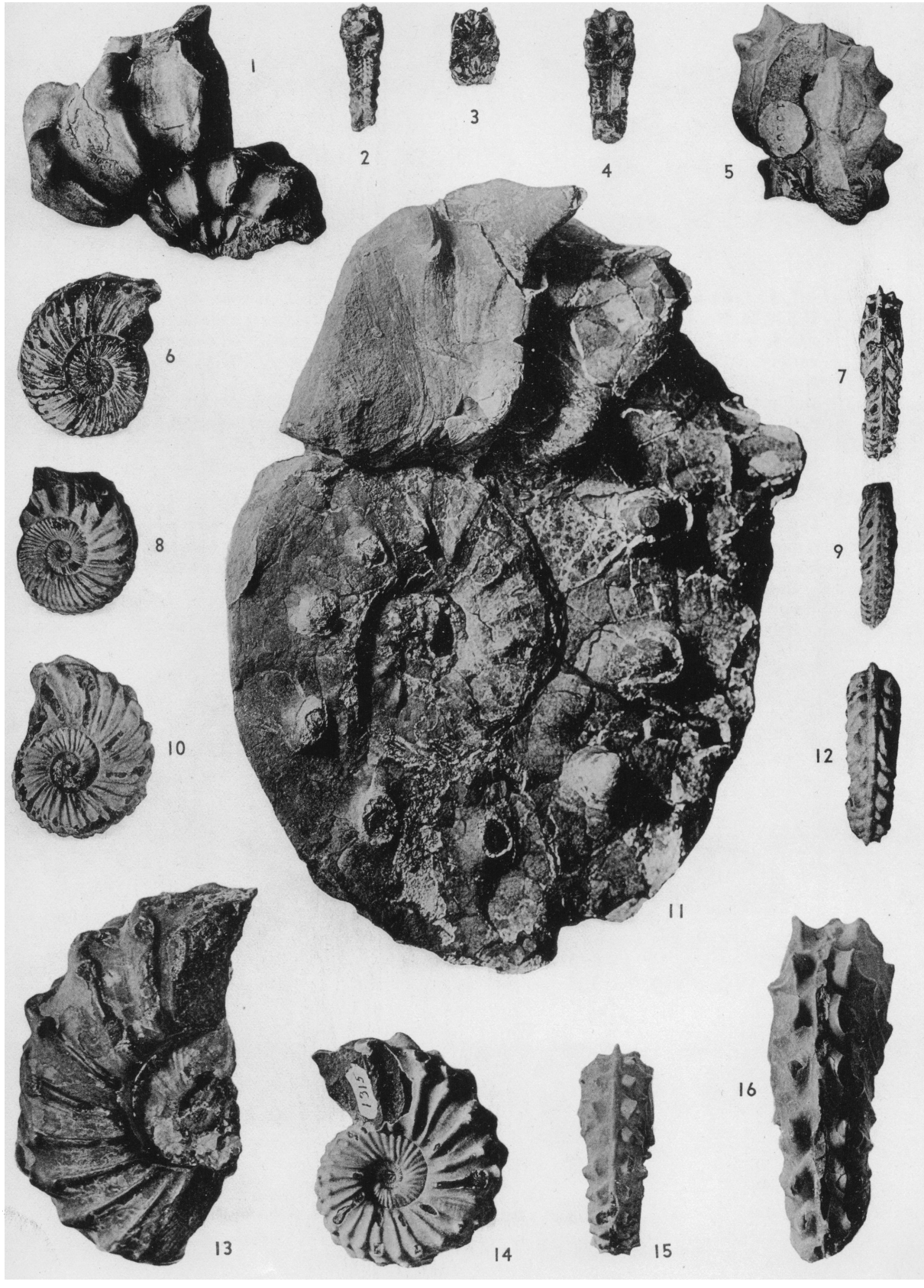
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PLATE 14

1, 5. *Prionotropis woollgari* Meek (? *non* Mantell), var. *crassa*, new variety. Holotype, U.S.N.M. No. 103916; 1, right side view, 5, ventral view (illustrating nodal section also).

2–4, 6–10, 12–16. *Prionotropis woollgari* Meek (? *non* Mantell), var. *intermedia*, new variety. 2, Paratype U.S.N.M. No. 103896m, sectional view. 3, Paratype U.S.N.M. No. 103896n, section at anterior end of fragment. 4, Paratype U.S.N.M. No. 103896l, sectional view. 6, 7, Paratype U.S.N.M. No. 103896d; 6, right side view; 7, ventral view. 8, 9, Paratype U.S.N.M. No. 103902d; 8, left side view; 9, ventral view. 10, 12, Paratype S.D.S.S.M. No. 1672a; 10, left side view, 12, ventral view. 13, 16, Paratype U.S.N.M. No. 103911; 13, right side view; 16, ventral view. 14, 15, Holotype, S.D.S.S.M. No. 1315; 14, left side view, 15, ventral view.

11. *Prionotropis woollgari* Meek (? *non* Mantell), *forma typica*? A.M.N.H. No. 25986: 1; left side view of largest disk, ×$\frac{1}{2}$, taken somewhat obliquely to show last horn, which is deprived of the test (see p. 172, footnote); thickness of test can be seen below that horn. Note, furthermore, apertural margin and growth striae running parallel to it.

Unless otherwise indicated, all figures are natural size.

For horizons and localities, see pages 197, 198.

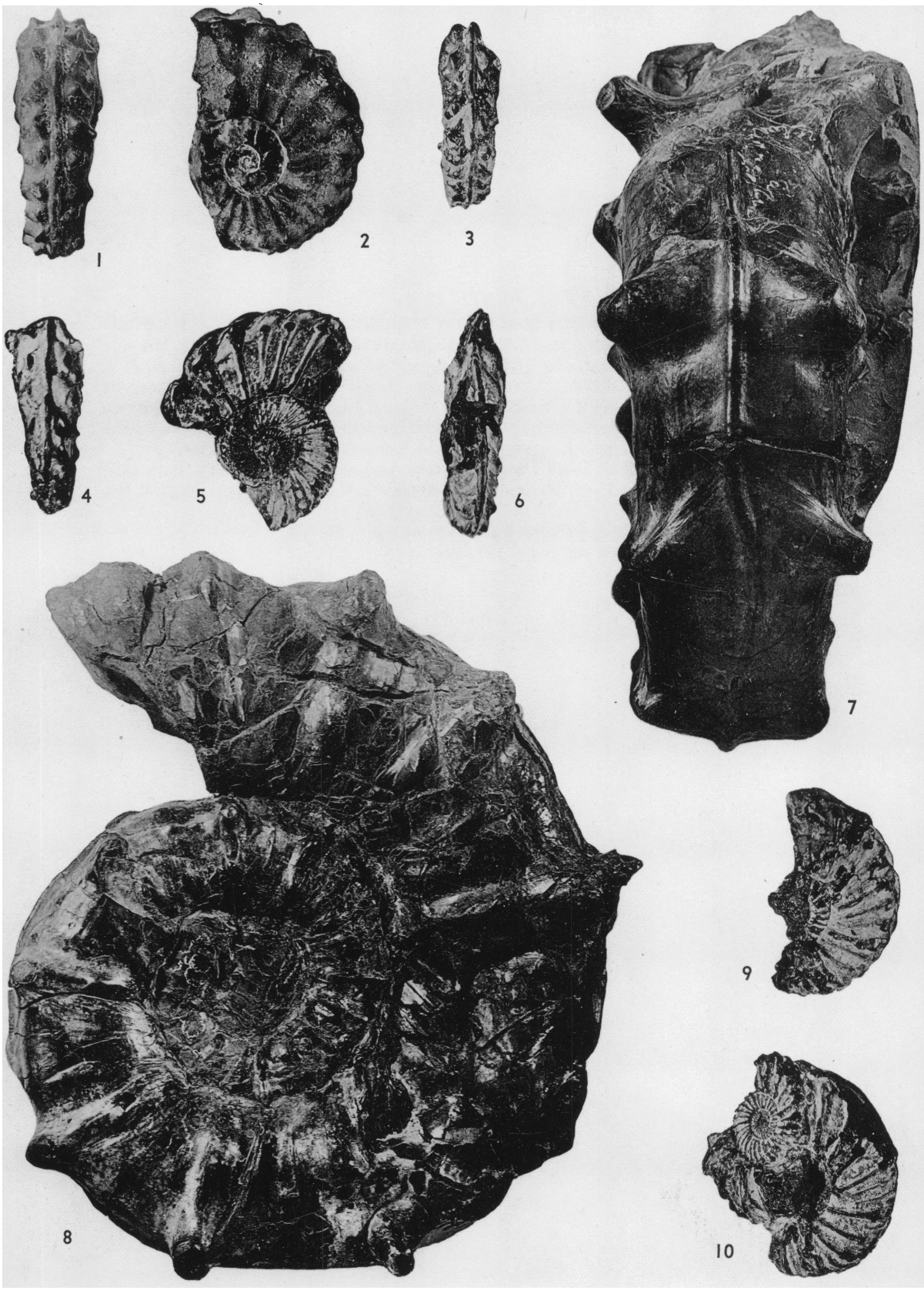
PLATE 15

1–6, 9, 10. *Prionotropis woollgari* Meek (? *non* Mantell), var. *intermedia*, new variety. 1, 2, A somewhat aberrant paratype, S.D.S.S.M. No. 1672b; 1, ventral view; 2, left side view. 4, 5, Paratype U.S.N.M. No. 103896h; 4, ventral view; 5, right side view. 3, 9, Paratype U.S.N.M. No. 103896f; 3, ventral view; 9, left side view. 6, 10, Paratype U.S.N.M. No. 103896g; 6, ventral view, slightly oblique; 10, left side view; note the two secondary ribs intercalated at about the middle of the half whorl; the specimen to the right, attached to this half whorl, is referred to the *forma typica* of this species.

7, 8. *Prionotropis woollgari* Meek (? *non* Mantell), var. *crassa*, new variety. Paratype, U.N.S.M. No. 1-12-12-37; 7, ventral view of posterior half of outer whorl, $\times\frac{1}{2}$; 8, left side view, $\times$ *ca.* $\frac{2}{3}$.

Unless otherwise indicated, all figures are natural size.

For horizons and localities, see pages 197, 198.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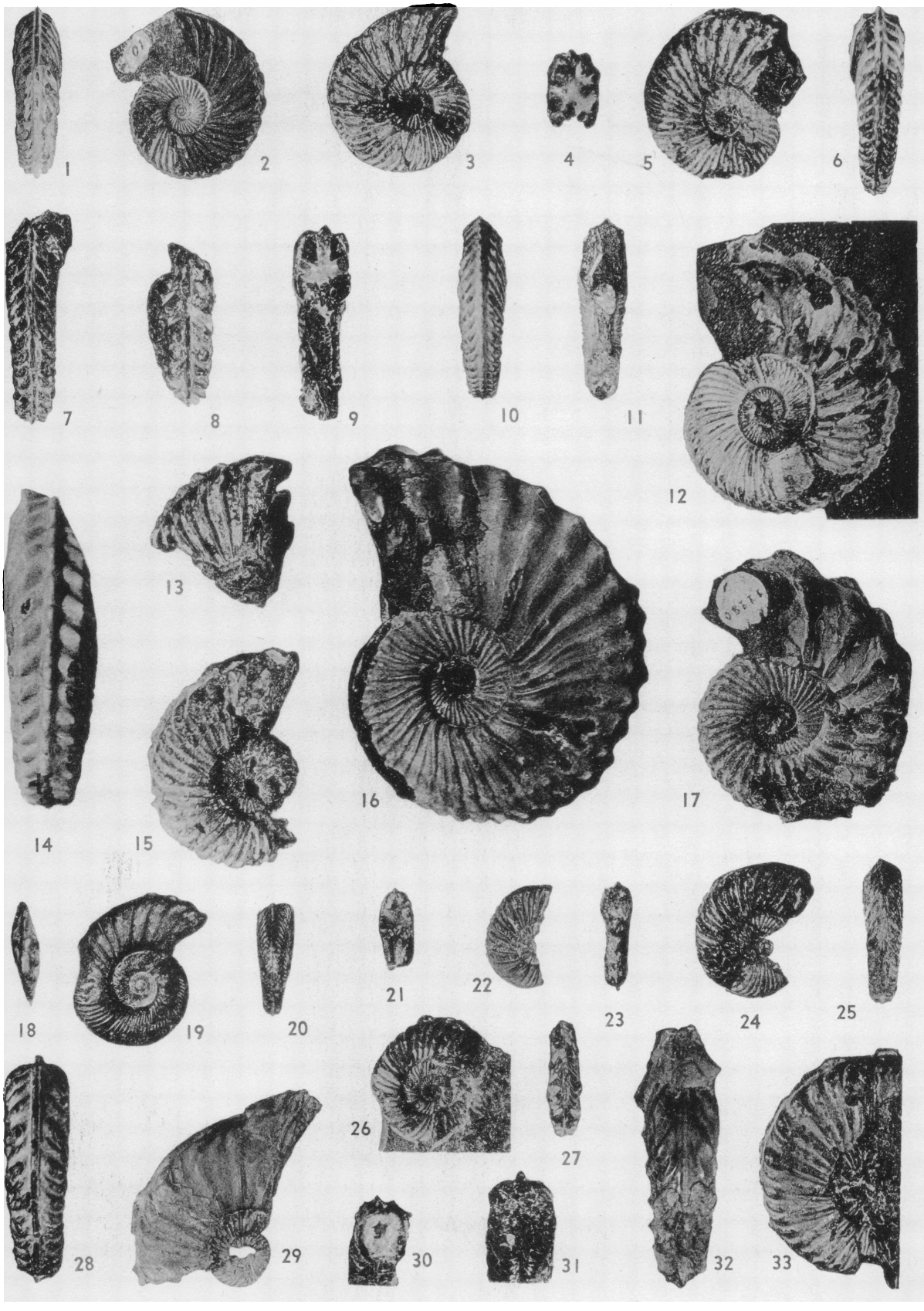
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PLATE 16

1–17. *Prionotropis woollgari* Meek (? *non* Mantell), var. *regularis*, new variety. 1, 2, Paratype S.D.S.S.M. No. 1074a; 1, ventral view; 2, left side view. 3, Paratype U.S.N.M. No. 103897i, right side view. 4, Paratype U.S.N.M. No. 103897g, section at fracture, ×2. 5, 6, Paratype U.S.N.M. No. 103897a; 5, right side view; 6, ventral view. 7, 15, Paratype U.S.N.M. No. 103897e; 7, ventral view; 15, right side view. 8, 13, Paratype U.S.N.M. No. 103897h; 8, ventral view; 13, right side view. 9, Paratype U.S.N.M. No. 103897d, sectional view. 10–12, Paratype U.S.N.M. No. 103903a; 10, ventral view of posterior half of outer whorl; 11, sectional view at fracture (recognizable in fig. 12); 12, left side view. 14, 16, Holotype, S.D.S.S.M. No. 1470; 14, ventral view; 16, left side view. 17, Paratype U.S.N.M. No. 103903b, left side view.

18–21. *Prionotropis woollgari* Meek (? *non* Mantell), var. *tenuicostata*, new variety. 18–20, Holotype, U.S.N.M. No. 103904; 18, ventral view of anterior part of outer whorl (illuminated from the right side to improve distinctness); 19, right side view; 20, ventral view of posterior half of outer whorl. 21, Paratype U.S.N.M. No. 103898a, sectional view.

22–33. *Prionotropis woollgari* Meek (? *non* Mantell), var. *praecox*, new variety. 22, 23, Paratype U.S.N.M. No. 103913c; 22, right side view; 23, sectional view. 24, 25, Paratype U.S.N.M. No. 103906a; 24, right side view; 25, ventral view. 26, 27, Paratype U.S.N.M. No. 103913g; 26, right side view; 27, ventral view. 28, 31, 33, A somewhat aberrant paratype, U.S.N.M. No. 103913f; 28, ventral view; 31, section near anterior end; 33, right side view. 29, 32, Paratype U.S.N.M. No. 103913b; 29, right side view; 32, ventral view. 30, Paratype U.S.N.M. No. 103906c, section at fracture (near beginning of outer whorl).

Unless otherwise indicated, all figures are natural size.

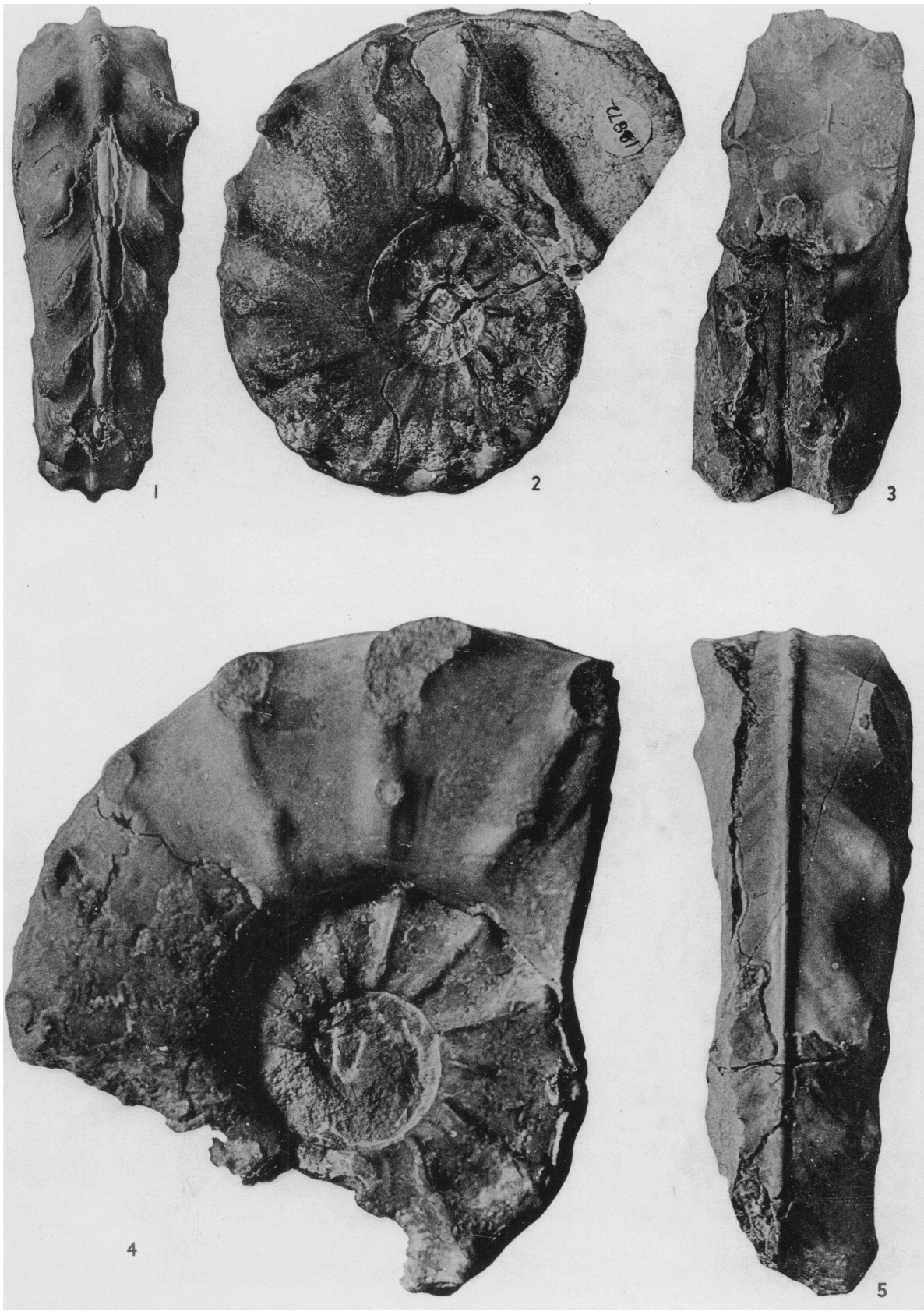
For horizon and localities, see pages 197, 198.

PLATE 17

Prionotropis woollgari Meek (? *non* Mantell), var. *praecox*, new variety. 1, 2, Holotype, U.S.N.M. No. 103913; 1, ventral view; 2, right side view. 3–5, Largest paratype, U.S.N.M. No. 103913e; 3, sectional view at fracture (recognizable in fig. 4); 4, right side view; 5, ventral view.

All figures are natural size.

For horizons and localities, see page 198.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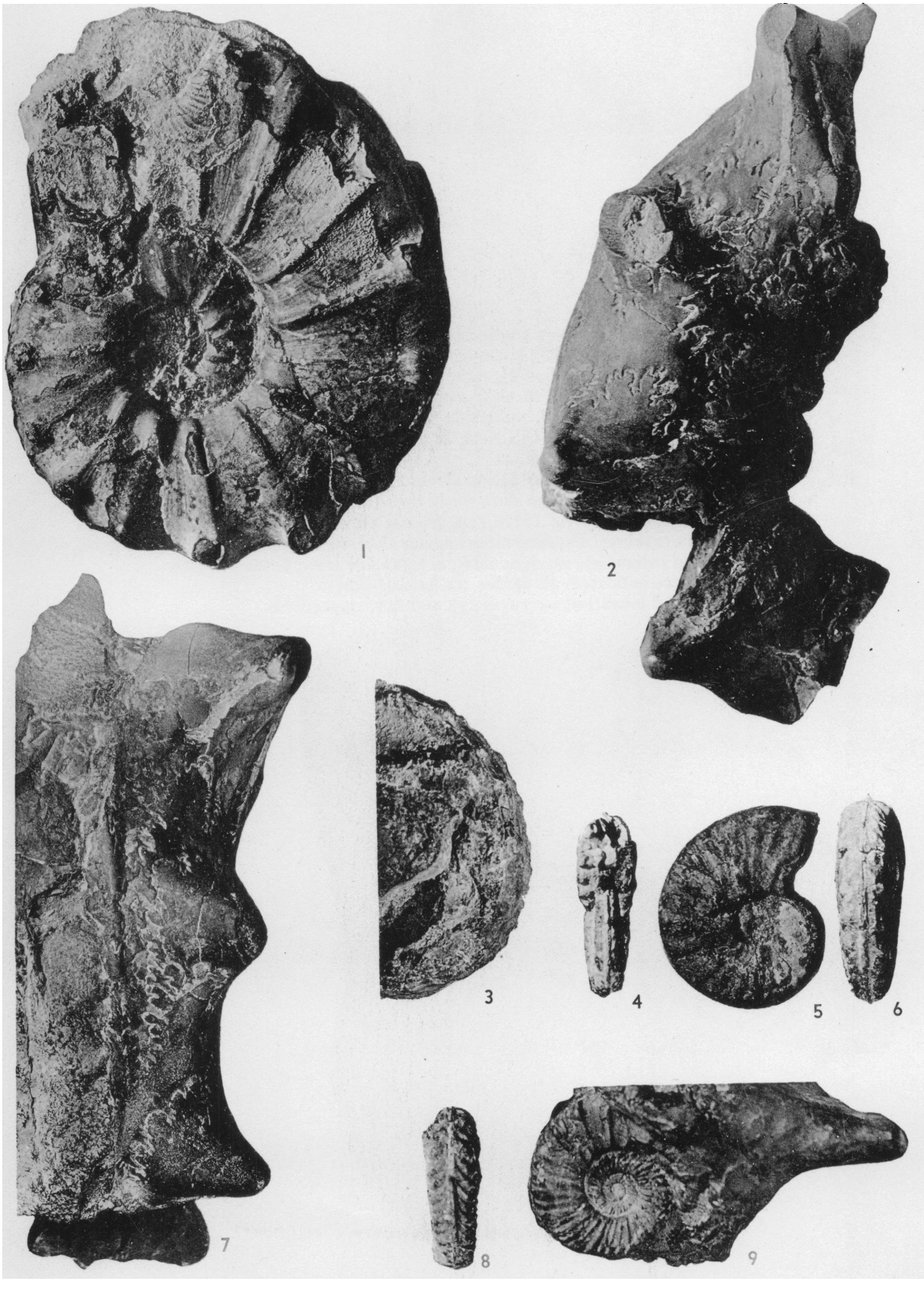
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PLATE 18

1, 8, 9. *Prionotropis woollgari* Meek (? *non* Mantell), var. *praecox*, new variety. 1, Paratype U.S.N.M. No. 103906b, left side view. 8, 9, Paratype U.S.N.M. No. 103913d; 8, ventral view; 9 (left side of figure), right side view.

2, 7, 9. *Prionotropis woollgari* Meek (? *non* Mantell), var. *alata*, new name. 2, 7, Paratype U.S.N.M. No. 103912a; 2, right side view, slightly reduced; 7, ventral view. 9 (Right side of figure), paratype U.S.N.M. No. 103912b, a single left horn from a large shell, seen obliquely and upside down.

3–6. *Prionocyclus wyomingensis* Meek, *forma typica*. 3, A.M.N.H. No. 25926:5, left side view of penultimate whorl, to show finely denticulate keel. 4–6, The smallest specimen of the lot, A.M.N.H. No. 25926:1; 4, frontal view, somewhat reduced and inaccurate (right lateroventral shoulder more angular than appearing at upper left of figure, and its lower end incomplete on right side); 5, right side view; 6, ventral view.

Unless otherwise indicated, all figures are natural size.

For horizons and localities, see pages 198 and 215, respectively.

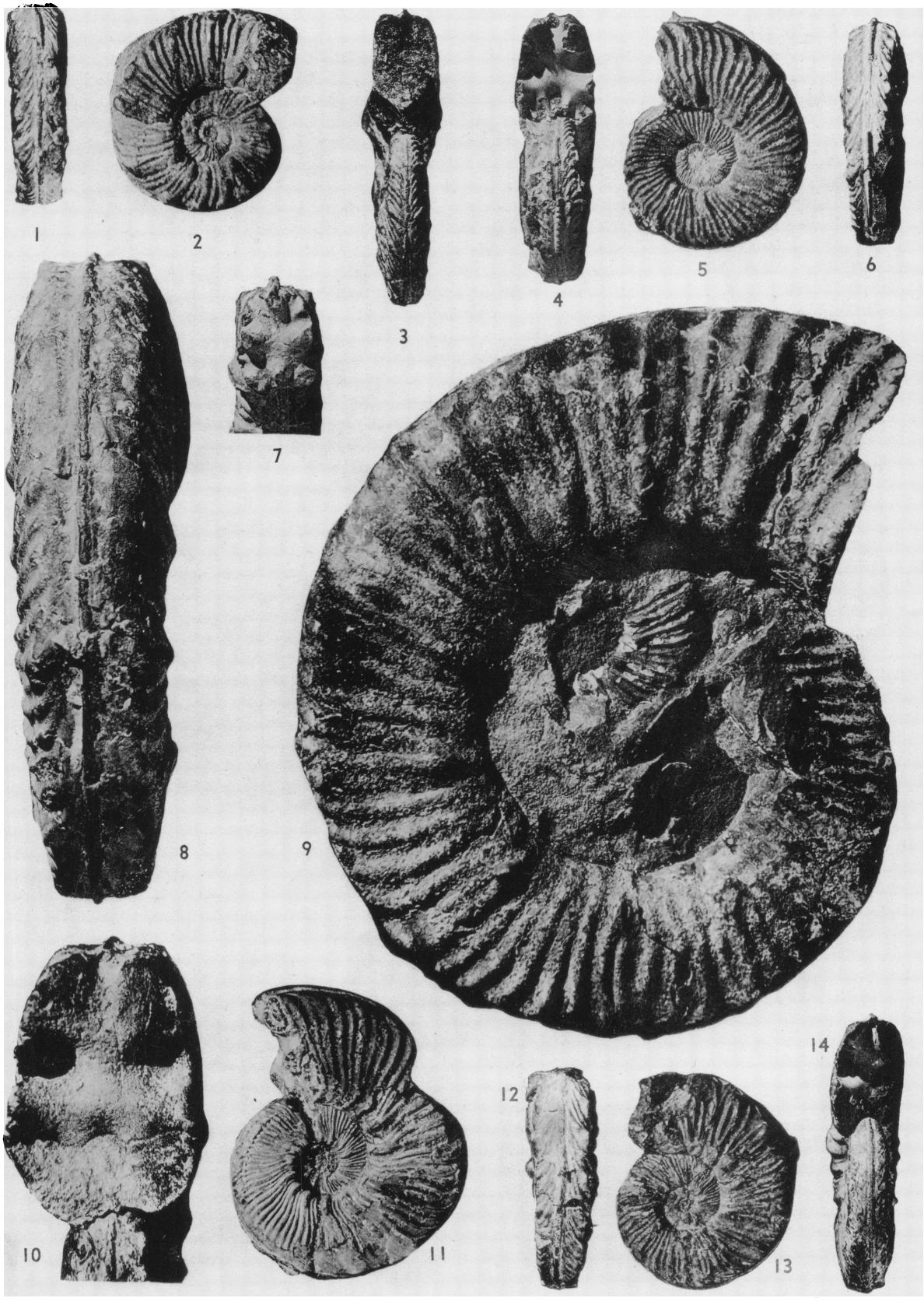
PLATE 19

1–7, 11–14. *Prionocyclus wyomingensis* Meek, var. *elegans*, new name. 1, 2, Paratype A.M.N.H. No. 25503:1; 1, ventral view, showing occasional indications of twin nodes; 2, right side view. 3, Paratype A.M.N.H. No. 25503:3, frontal view, ×$\frac{3}{2}$, to show slenderness of conch and fineness of ornamentation. 4–6, Paratype Col. Univ. No. 10630a; 4, frontal view, ×$\frac{3}{2}$, to show fineness of ornamentation and, in lower part of figure, serration of keel; 5, left side view; 6, ventral view; figures 4–6 taken after removal of foremost part of outer whorl. 7, 12, 13, Paratype A.M.N.H. No. 25503:2; 7, section at fracture (recognizable in fig. 13), ×$\frac{3}{2}$; 12, ventral view; 13, left side view. 11, 14, Paratype A.M.N.H. No. 25503:4; 11, left side view; 14, frontal view, showing extreme fineness of ornamentation on venter.

8–10. *Prionocyclus wyomingensis* Meek, *forma typica*. A.M.N.H. No. 25926:4; 8, ventral view; 9, right side view; 10, section at anterior end.

Unless otherwise indicated, all figures are natural size.

For horizons and localities, see page 215.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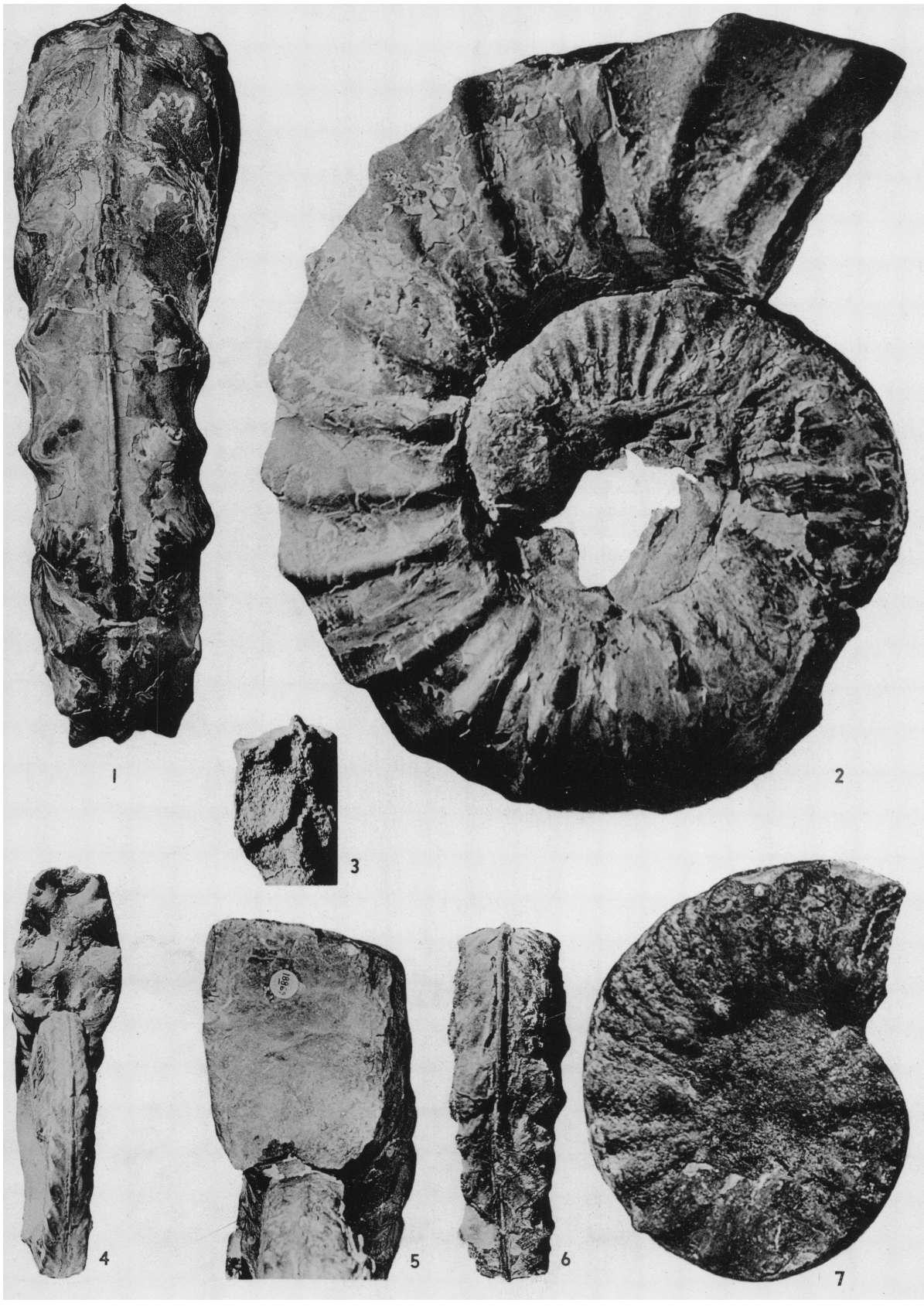
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PLATE 20

1, 2, 5. *Prionocyclus wyomingensis* Meek, *forma typica*. Largest specimen on record, U.S.N.M. No. 103677; 1, ventral view; 2, right side view; 5, section at anterior end; all three $\times\frac{1}{2}$.

3, 6, 7. *Prionocyclus wyomingensis* Meek, var. *robusta*, new variety. Smallest paratype, A.M.N.H. No. 25928:1; 3, section at anterior end; 6, ventral view; 7, right side view.

4. *Prionocyclus wyomingensis* Meek, var. *elegans*, new name. Paratype A.M.N.H. No. 25912:2, frontal view.

Unless otherwise indicated, all figures are natural size.

For horizons and localities, see page 215.

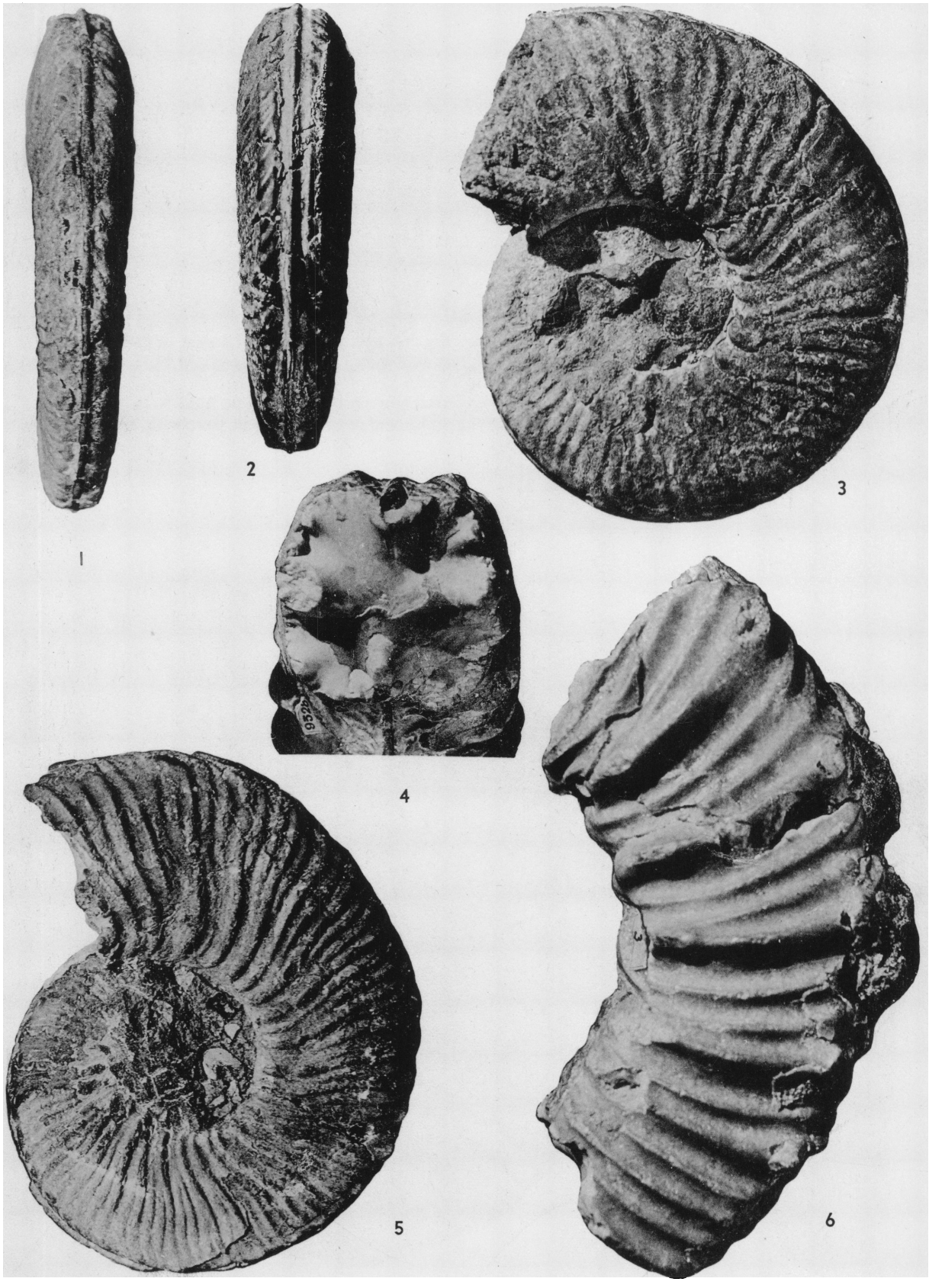
PLATE 21

1–3, 5. *Prionocyclus wyomingensis* Meek, var. *elegans*, new name. 1, 5, Largest paratype, S.D.S.S.M. No. 1507; 1, ventral view; 5, left side view. 2, 3, Paratype A.M.N.H. No. 25912:4; 2, ventral view; 3, left side view.

4, 6. *Prionocyclus wyomingensis* Meek, var. *robusta*, new variety. Paratype A.M.N.H. No. 9528/3; 4, section at posterior end, showing siphuncular tube, filled in part with a dark core (keel broken off); 6, left side view.

All figures are natural size.

For horizons and localities, see page 215.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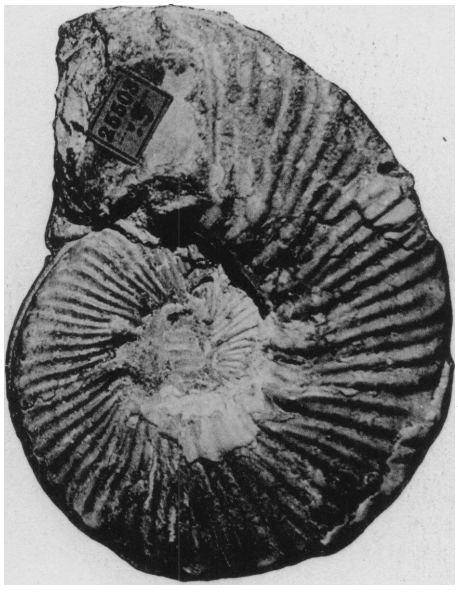

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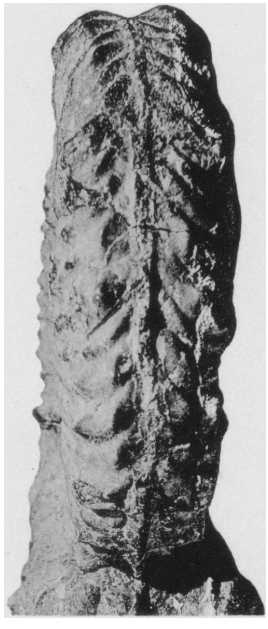

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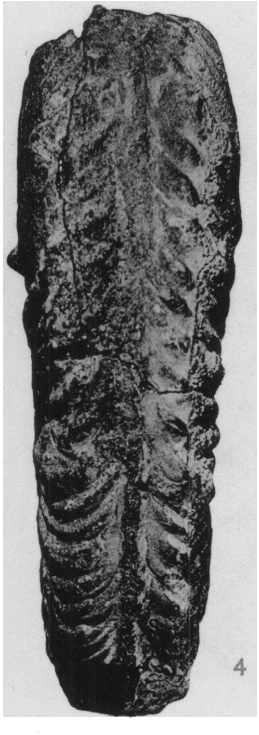

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PLATE 22

1, 2. *Prionocyclus wyomingensis* Meek, var. *elegans*, new variety. Paratype A.M.N.H. No. 25503:5; 1, left side view; 2, ventral view.

3–5. *Prionocyclus wyomingensis* Meek, var. *robusta*, new variety. Holotype, A.M.N.H. No. 25928:2; 3, ventral view of posterior half of outer whorl, showing strongly developed twin nodes; 4, ventral view of anterior quarter of outer whorl; 5, right side view; all three ×$\frac{1}{2}$.

Unless otherwise indicated, all figures are natural size.

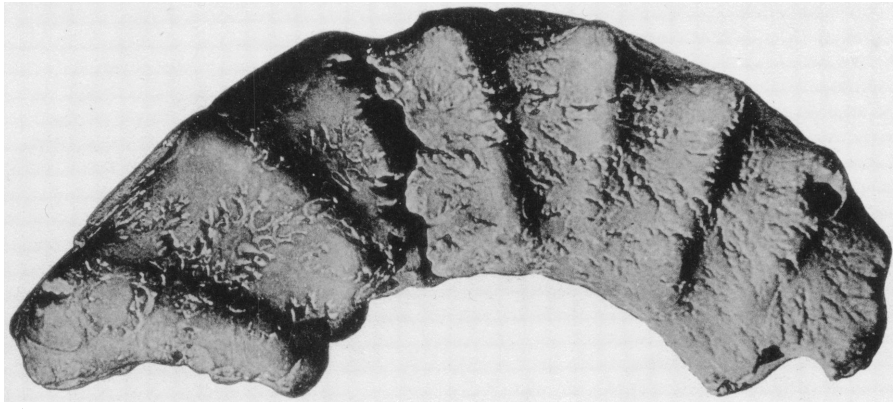
For horizons and localities, see page 215.

PLATE 23

1, 3. Combined figures, to show homeomorphy, of *Prionocyclus* cf. *wyomingensis* Meek, A.M.N.H. No. 25469 (anterior fragment), and *Pervinquieria romeri* Haas, paratype, A.M.N.H. No. 25141:1 (posterior fragment); 1, ventral view; 3, left side view; both $\times\frac{1}{2}$.

2. *Prionocyclus wyomingensis* Meek, var. *robusta*, new variety. Paratype A.M.N.H. No. 9528/1, right side view, natural size.

For horizons and localities of A.M.N.H. Nos. 9528/1 and 25469, see page 215. A.M.N.H. No. 25141:1 is from the Albian of Hanha, near Lobito, Angola.



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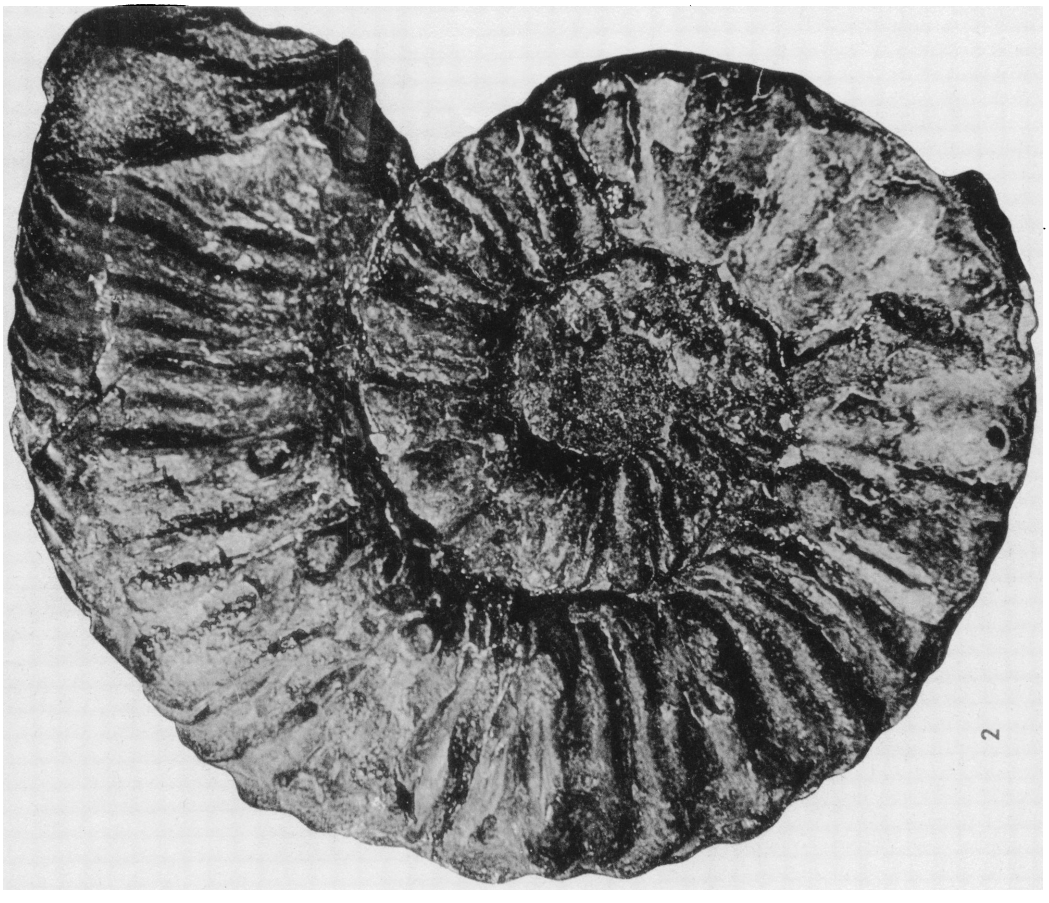

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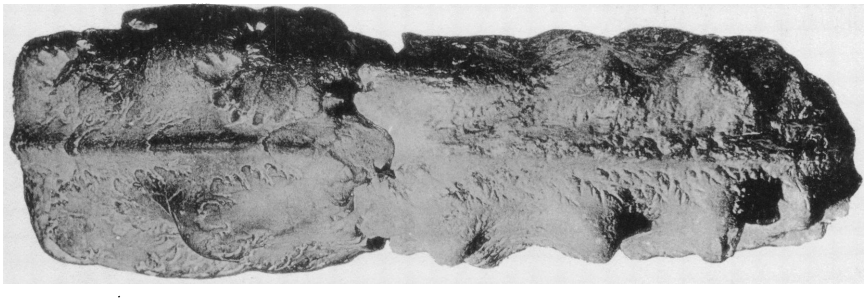

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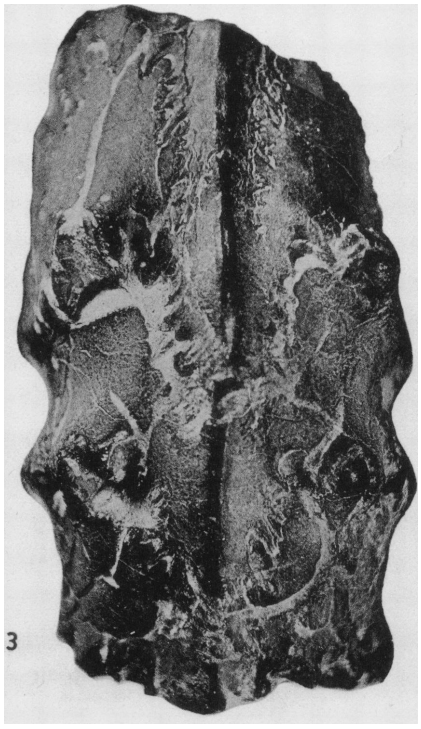

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PLATE 24

1. Side view of the "unnumbered block" of the United States National Museum; natural size. Compare plates 11, 12.

2, 3. *Prionocyclus wyomingensis* Meek? The larger one of the two fragments U.S.N.M. No. 103676 from the Mancos shale of Antonio Sedillo Grant, near Suwannee, Valencia County, New Mexico; 2, right side view; 3, ventral view; both ×½.