ALBIAN AMMONITES FROM FOSSIL CREEK, OODNADATTA, SOUTH AUSTRALIA

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[Read 9 April 1964]

SUMMARY

Fifteen species of ammonites, of which one is new, are recorded from the South Australian part of the Albian sequence in the Great Artesian Basin at Fossil Creek, 30 miles west-north-west of Oodnadatta. Thirteen of the species are heteromorphs. They are assigned to *Labeceras* s. str., *L.* (*Appurdiceras*) and to *Myloceras*. The non-heteromorphic species belong to *Falciferella*. Connections with New Guinea are confirmed and relationships with the Albian of Portuguese East Africa pointed out. The descriptive presentation is supported by some simple bivariate biometric analyses. Remarks on the nekroplanktonic dispersal of heteromorphic ammonites are made. The currently accepted correlation of the beds containing heteromorphs on the international zonal scale is confirmed.

INTRODUCTION

It is some 60 years since the first Albian ammonites were described from South Australia by Etheridge (1905). Later work on the Queensland extensions of the Great Artesian Basin disclosed the presence of a multitude of forms, largely heteromorphic; these could be tied up with a few earlier discoveries, including a small but important collection from New Guinea. The occurrence of certain species of the genera *Prohysteroceras* and *Mortoniceras* permitted incorporation of the Australian occurrences in the international zonal scheme. This was indeed fortunate, as it had not been possible to base correlation on the unique uncoiled forms, at least not at that time.

There seems to have been a lull in interest in the South Australian Lower Cretaceous, until the exploration for oil in the Great Artesian Basin once again provided the necessary incentive to further work. Up to the early fifties the South Australian ammonite faunas were badly known and it might have been thought strange that there was so little agreement with the sequence in Queensland. However, it is now possible to demonstrate complete faunal agreement between the two areas.

The material described and figured in the present paper has been deposited in the collections of the Geological Survey of South Australia, Adelaide.

LOCATION OF THE AREA

The area lies at about the intersection of 27° south latitude and 134° east longitude. The fossils were obtained from exposures in the Fossil or Wooldridge Creek, which lies roughly 30 miles west-north-west of Oodnadatta.

The ammonites were collected by the following people: Dr. R. O. Brunnschweiler (1955), Dr. H. Wopfner, Mr. A. Hess and Mr. D. Scott (1956), as well as officers of the Geological Survey of South Australia, among them Mr. J. Johnson.

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DESCRIPTIVE SECTION

Family LABECERATIDAE Spath, 1925

(Syn. *Aleteceratidae*, Whitehouse (1925), *Myloceratidae*, Spath (1939))

The encompassment given by Wright (1956) in the Treatise of Invertebrate Paleontology is here observed. The family is then considered to comprise heteromorphs which are at first coiled in an open spiral, but later whorls may be in contact, the shell terminating in a hook. The aperture is provided with weak to moderately prominent, rounded lappets. The whorl section is moderately to fairly strongly compressed. All genera have fine, branching ribs that cross the venter. Umbilical or ventrolateral tubercles, or both, occur. The suture consists of bifid saddles and smallish bifid lobes.

Genus LABECERAS Spath, 1925

Type Species.—*Labeceras bryani* Whitehouse, 1926.

Description.—Rather small shells with an open spire of a few whorls, followed by a curved shaft and a final hook, with the aperture usually facing inward. The ribs are fine, slightly sinuous and lean forwards; occasionally they bifurcate. Umbilical tubercles may occur on the shaft and hook, as also ventrolateral tubercles.

Age.—Albian.

Subgenus LABECERAS

Remarks.—*L.* (*Labeceras*) is considered to comprise forms lacking ventrolateral tubercles.

Labeceras (Labeceras) laqueum (Etheridge)

Pl. 1, Fig. 1

1892 *Hamites* (or *Hamulina*?) *laqueus*, Etheridge, p. 496, pl. 42, figs. 14, 15.

1909 *Crioceras taylori* (in part), Etheridge, pl. 49, fig. 4.

1926 *Labeceras laqueus* (Etheridge fil.), Whitehouse, p. 227.

1926 *Labeceras papulatum*, Whitehouse, p. 228, pl. 36, fig. 4; pl. 39, figs. 3a-b.

Description.—This species is characterized by the dense ribbing and its tendency, on the body chamber, to weaken, become less dense and to develop tubercles on the umbilicus. The whorl section is inflated oval, the venter is smoothly rounded. The last 4·5 cm up to the last suture have 33 ribs, counted on the venter (a rib density of $\epsilon = 7\cdot 3/\text{cm}$).

Remarks.—There are genuine differences between this species and *L.* (*L.*) *bryani* Whitehouse with respect to the ribbing. The specimen studied has part of the altered shell material preserved on the umbilical area — here umbilical tubercles occur, whereas on the other (figured) side, on which the shell is missing, tubercles are only suggested. It would therefore seem that the presence or absence of tubercles on the body chamber is largely a matter of preservation, although infraspecific variation certainly plays a part.

Material.—One specimen, M 1439.

Labeceras (Labeceras) crassum Spath.

Pl. 1, Fig. 2

1892 *Crioceras* sp. Etheridge, p. 502, pl. 33, fig. 4.
1909 *Crioceras laqueus,* Etheridge, pl. 49, figs. 7 and 9 (not fig. 8).
1925 *Labeceras plasticum* sp. nov. var. *crassa,* Spath, p. 191, pl. 34, figs. 5-7.
1926 *Labeceras trifidum,* Whitehouse, p. 228.
?1958 *Labeceras trifidum* Whitehouse, Glaessner, p. 218, pl. 26, figs. 4a-c.

Description.—None of the specimens available is complete. The species is characterised by clavate umbilical tubercles on the body chamber, from which the ribs proceed in bundles of twos and threes. Two fragments may be from the septate part of the shell; these are also provided with umbilical tubercles, but these lie further down on the dorsolateral shoulders. The whorl sections of these two smaller fragments are subquadrate, whereas that of the body chamber is almost round.

Material.—Three specimens. M 1440, M 1441, M 1442.

Remarks.—Whitehouse (1926, p. 229) thought that the septate part of the shell of this species might not be tuberculate. The evidence of the present material, although not absolutely conclusive, suggests that the contrary may be true. It is still not possible to give a picture of the suture line; however, the fragment of the body chamber also has the last septal surface preserved. From this it may be inferred that the central lobe is narrow, the external saddle very broad, the first lateral saddle is narrow, but not as narrow as the ventral lobe, and the first lateral saddle is also broad. This accords well with the general form of the labeceratid suture. The ribbing of the form referred here by Glaessner (1958) appears coarser and the ridges formed by the saddles on the septal surface are wider than our material. Nevertheless, the original figures of Etheridge (1909, p. 49, figs. 7 and 9) indicate variability with respect to costation. The East African material figured by Spath (1925) agrees closely with the Australian.

Biometric Analysis.—It has already been observed that there appears to be variation with respect to the ontogeny of the whorl section of *L. crassum.* Measurements on maximum whorl height and whorl breadth were made and these

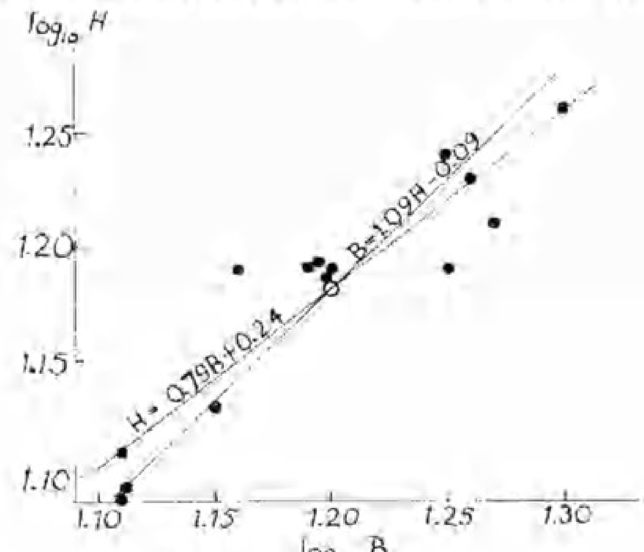

Fig. 1. Covariation in whorl breadth and whorl height of *Labeceras crassum* Spath.

were then subjected to regression analysis. It is worth mentioning that the whorl dimensions do not increase regularly and there are frequent slight diminutions shown by the largest specimen. In text Fig. 1 a plot of $\log_{10}$ (breadth) against $\log_{10}$ (height) is shown together with the regression lines of the data. The logarithmic transformation is necessary as the measurements are non-linear, thus indicating differential growth. The correlation coefficient between the transformed variables is 0·926, which is highly significant.

Labeceras (Labeceras) compressum Whitehouse

Pl. 1, Figs. 3-4

1926 *Labeceras compressum*, Whitehouse, p. 228, pl. 36, fig. 5; pl. 39, figs. 5a-b.

Description.—This species is characterised by the compressed whorl section, the numerous, thin ribs, which lean slightly forwards on the shaft of the body chamber but straighten up on the hook thereof, and the rather tight bend of the crook. The ribs may bifurcate at the dorsolateral margin or in the outer third of the flanks. The rib density of the body chamber studied is $\epsilon = 7{\cdot}7$/cm. The lappets run from the dorsolateral shoulder to the beginning of the outer third of the flanks. The suture line has a relatively broad external lobe, a broad external saddle with a rather well developed median sublobe, a broad first lateral lobe and a first lateral saddle of about the same width as the first lateral lobe.

Material.—Two specimens. M 1415, M 1443.

Remarks.—Unfortunately, the photograph of the holotype supplied by Whitehouse (1926, p. 29, fig. 5a) is indistinct so that the details of the ribbing cannot be made out. However, the distinctive development of the lappets is clear, as also the compressed whorl section.

Labeceras (Labeceras) oodnadattaensis sp. nov.

Pl. 1, Fig. 5

Holotype.—A complete specimen, M 1444 and M 1445, figured in Pl. 1, Fig. 5.

Diagnosis.—A species of *L.* (*Labeceras*) with the following characteristics: Whorl section strongly compressed, sigmoidal ribbing, simple and bifurcated, leaning slightly forward, aperture not turned in towards shaft.

Description.—The coiling is ancyloceratid, the tip of the shell lying only about 1 mm. from the shaft. The body chamber takes up just less than one-half of the total shell length (= 0·47 of total length). The shell heightens rapidly (see text Fig. 2) during the first part of its length and thereafter the increase is less rapid. Height increase ceases around the hook of the shell, where periods of decrease in height also occur. The rib density is $\epsilon = 6{\cdot}5$/cm. The ribs are slightly flexed; they widen slightly outwards. Most ribs bifurcate either at the dorsolateral margin or at the outer third of the flank, but simple ribs also occur. The aperture is not directed towards the shaft, but faces instead outwards. The suture line is typical of *Labeceras*. Maximum length = 62 mm.

Material.—One complete specimen. This specimen is in two parts, the one an almost complete mould, lacking the first part of the shell, the other partly the impression of the shell, but bearing the first part of the shell.

Remarks.—The new species is most closely related to *L.* (*L.*) *compressum* Whitehouse, but differs in the following important aspects. The ribbing of

L. (*L.*) *oodnadattaensis* sp. nov. is somewhat coarser, the ribs are more sigmoidal and have a tendency to become club-shaped, the shell is smaller, and the aperture does not face inwards. The specimen is figured in its nekroplanktonic floating position in Pl. 1, Fig. 5.

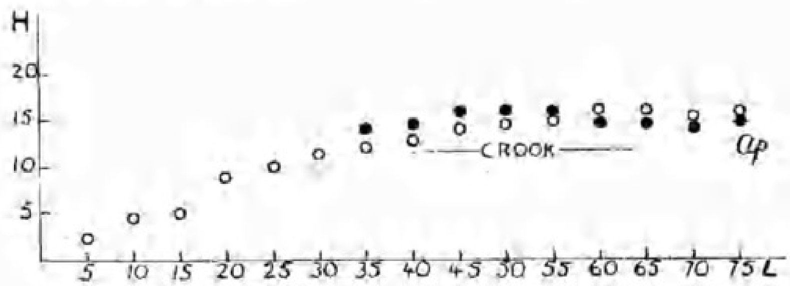

Fig. 2. Ontogeny of whorl height shown for 5 mm intervals of length for *Labeceras* (*Labeceras*) *oodnadattaensis* sp. nov. (open circles). The development of the body chamber of *L.* (*L.*) *compressum* Whitehouse (filled dots) is shown for comparison. Ap denotes the end of the body chamber. Measurements in mm.

Subgenus Appurdiceras Whitehouse, 1926

Type Species.—*Ancyloceras cordycepoides* Etheridge, 1905.

Description.—Ancyloceratidally coiled whorls with rounded subquadrate to rounded subrectangular whorls. The ribs are mainly simple but occasional bifurcation may occur. Some ribs bear ventrolateral tubercles.

Labeceras (Appurdiceras) cordycepoides (Etheridge)

Pl. 1, Figs. 6 and 7

1905 *Ancyloceras cordycepoides*, Etheridge, p. 14, pl. 1, figs. 3-5; pl. 2, fig. 4(?).

1926 *Appurdiceras cordycepoides* (Etheridge fil.), Whitehouse, p. 230.

Description.—This species is characterised by its subquadrate to circular whorl section, and the stout, only occasionally bifurcated ribs, which lean forwards, about every fifth of which is provided with a strong, spinate ventrolateral tubercle. The ribbing appears to become denser on the body chamber.

Material.—Two specimens. M 1446, M 1447.

Genus Myloceras Spath, 1925

(Syn. *Aleteceras*, Whitehouse, 1926, *Flindersites*, Whitehouse, 1926).

Type Species.—*Crioceras ammonoides* Etheridge, 1909.

Description.—Shells larger than *Labeceras* s. l. with the spire either crioceratid or ancyloceratid and more closely coiled than *Labeceras*; at some stage of development some whorls are in contact. The aperture does not face inward to the same degree as in most *Labeceras*. The whorl section varies from strongly compressed to strongly depressed. Ventrolateral tubercles may occur.

Remarks.—The differences considered by Whitehouse (1926) to be of generic importance in separating *Myloceras*, *Aleteceras*, *and Flindersites* are so slight as to be hardly of specific importance. In the present connection, therefore, the procedure adopted by Wright (1957) is adhered to and all are grouped under *Myloceras* Spath.

Myloceras nautiloides (Etheridge)

Pl. 2, Figs. 1, 2; Text-Fig. 3

1909 *Criceras nautiloides*, Etheridge, p. 148, pl. 45, text-fig. 8.

1926 *Aleteceras nautiloides* (Etheridge fil.), Whitehouse, p. 233.

Description.—The whorls partly embrace. The body chamber has a depressed whorl section, the early septate part of the shell has a square whorl section, this becoming depressed while the shell is still septate. The septate whorls bear occasional ventrolateral tubercles (on about every sixth or seventh rib). The later septate part lacks tubercles. There are both simple and bifurcated ribs, simple ribs being most common on the body chamber. The shell wall is almost 3 mm. in thickness. A complete final suture is shown in Text Fig. 3.

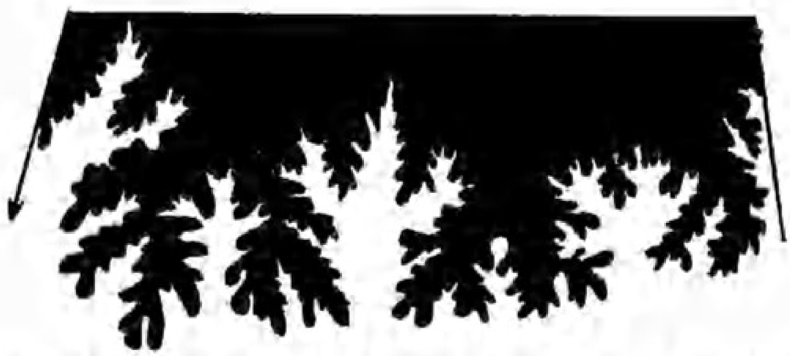

Fig. 3. Suture line of *Myloceras nautiloides* (Etheridge) M 1449 x 1.

Material.—Three specimens. M 1448, M 1449, M 1450 (3 pieces).

Remarks.—The material here described agrees with the specimen from Aramac, Queensland, very well. The depressed whorl section of the body chamber serves to distinguish the species well from other *Myloceras*.

Biometric Analysis.—The ontogeny of the whorl section was studied by plotting breadth of whorl against height of whorl (Text Fig. 4). There is obvious non-linearity in the data and it may be concluded that the growth rates for breadth and height change differentially with respect to each other. There is not sufficient material to permit a regression analysis.

Myloceras plectoides (Etheridge)

Pl. 2, Fig. 3; Pl. 5, Figs. 1, 2

1909 *Crioceras plectoides*, Etheridge, p. 152, pl. 33, fig. 2; pl. 46, fig. 1; pl. 47, figs. 1-4.

1926 *Aleteceras plectoides* (Etheridge fil.), Whitehouse, pl. 40, figs. 2a-c.

1926 *Aleteceras tardicostatum*, Whitehouse, p. 232, pl. 40, figs. 1a-c.

Description.—The whorl section of this species begins by being rather compressed but by about a diameter of 45 mm. it is almost subquadrate. Judging from the material at hand there also appears to be an ornamental change during the ontogeny in that the early part of the shell has slightly flexed ribs, these tending to become straighter, sharper, and slightly reclined at more advanced growth stages. There seems to be some variability concerning the point at which the ventrolateral tuberculation becomes apparent. The tubercles of the figured specimen in Pl. 2, Fig. 3, are feeble.

Material.—Mostly fragments. Nine specimens. M 1419, M 1451, M 1452, M 1453, M 1454, M 1455, M 1456, M1457.

Remarks.—Owing to the fact that there would appear to be a fair degree of variation in the strength of the ventrolateral tubercles of this species, it may not always be easy to pick it out. It seems likely that Whitehouse based his new species *tardicostatum* on the inner whorls of *plectoides*.

Myloceras baccatum (Whitehouse)

Pl. 2, Fig. 4

1909 *Crioceras flindersi* Etheridge (in part), pl. 36, fig. 2; pl. 41, fig. 3; pl. 42, fig. 2; pl. 44, fig 2.

1926 *Flindersites baccatus*, Whitehouse, p. 236.

Description.—The shell is large. The ribs are spaced, fairly strong and slightly flexed. There are moderately prominent, rounded ventrolateral tubercles. The ribs occasionally bifurcate at the dorsolateral margin, or unite at a ventrolateral tubercle. Two ribs proceed from each ventrolateral tubercle.

Material.—One specimen. M 1458.

Remarks.—In general appearance this species is not unlike *M. intermedium* (Whitehouse), but the specimen available is insufficient to permit accurate analysis. The figured specimen, which is crushed, shows a suite of sutures.

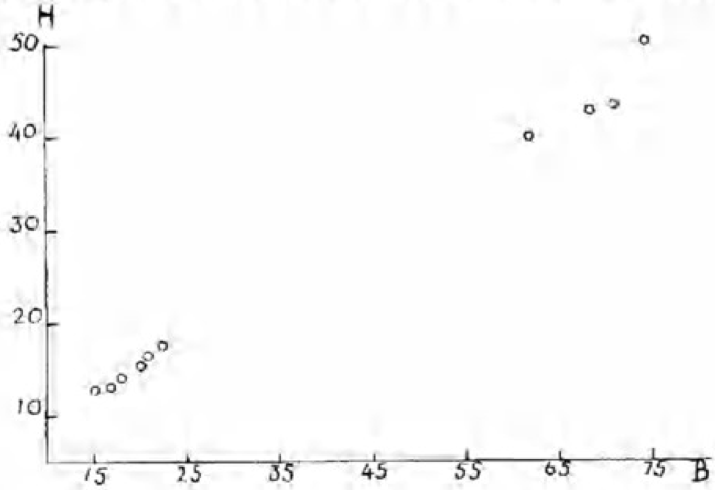

Fig. 4. Covariation in whorl breadth and whorl height for *Myloceras nautiloides* (Etheridge).

Myloceras intermedium (Whitehouse)

Pl. 1, Fig. 8

1909 *Crioceras flindersi* Etheridge (in part), pl. 40, figs. 1, 2.

1926 *Flindersites intermedius*, Whitehouse, p. 237.

Description.—This species has an almost rectangular whorl section, the venter is broad and arched. The ribs are thin, sharp and slightly flexed and lean strongly forwards. The ventrolateral tubercles are moderately strong and clavate. The ribs appear to be single on the flanks, but divide at the ventrolateral tubercles. On the dorsum the ribs sweep strongly forwards.

Material.—One specimen. M 1459.

Myloceras axonoides (Etheridge)

Pl. 3, Fig. 1

1909 *Crioceras axonoides*, Etheridge, p. 150, pl. 32, fig. 4; pl. 44, fig. 1.

1925 *Myloceras amaltheia*, Spath, p. 194, pl. 34, fig. 2.

1926 *Aleteceras*(?) *axonoides* (Etheridge fil.), p. 233.

Description.—This species is typified by the stout tuberculation of the septate whorls (the present material does not aid in clearing up the problem of whether the body chamber of the species really is non-tuberculate (cf. Spath, 1925, p. 194)), and the sharp nature of the costation, which leans slightly forwards.

Material.—A crushed fragment. M 1460.

Remarks.—Etheridge (1909, p. 151) definitely states the species to retain its tubercles throughout all growth stages, but this is not apparent from the figure. Spath distinguished his species *M. amaltheia* from *M. axonoides* on the basis of the non-tuberculation of the outer whorls of the latter and the "different" nature of the inner whorls of the two species. As far as is apparent from the illustration and our specimen there do not appear to be any significant differences. The specimen here figured agrees closely with the inner whorls of the specimen figured by Etheridge (1909, pl. 44, fig. 1).

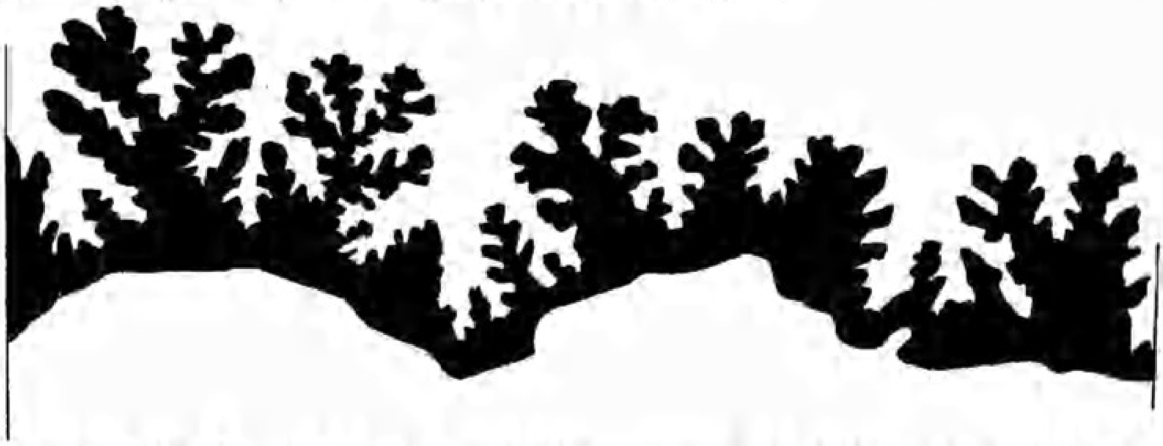

Fig. 5. Suture line of a large fragment of *Myloceras flindersi* (McCoy). M 1468. x1.

Myloceras flindersi (McCoy)

Pl. 3, Figs. 2, 3, Text Figs. 5, 6

1867 *Ancyloceras flindersi*, McCoy, p. 356.

1909 *Crioceras flindersi* Etheridge (in part), pl. 39, figs. 1, 2, 3.

1926 *Flindersites flindersi*, Whitehouse, p. 237.

1926 *Flindersites* aff. *flindersi* (McCoy), Whitehouse, p. 237.

Description.—This very large species is characterised by the clavate ventrolateral tubercle, which seem to disappear on the last parts of the body chambers of very large specimens and the sharp, though low, ribs, which may be almost straight to slightly flexed. After one turn the whorls are in contact. At a diameter of 19 mm. the ornament consists of single ribs, every fourth of which is provided with a spinate tubercle. Here the rib density is roughly $\epsilon = 8$/cm. A specimen with a radius of 46 mm. is somewhat more compressed than might be expected, but this may be a normal ontogenetic feature; it appears to have been slightly crushed. At this stage each rib bears an almost clavate tubercle and rib bifurcation is of frequent occurrence. Larger fragments are more

Fig. 6. Suture line of a fragment of *Myloceras* aff. *flindersi* (McCoy). M 1467, x0·75.

quadrate in whorl section. A large fragment of a septate specimen is similarly ornamented, but the whorl section is too depressed for it to be placed with *flindersi*. The suture of this specimen is figured in Text Fig. 6.

Material.—13 specimens. M 1461, M 1462, M 1463, M 1464, M 1465, M 1466, M 1467(?), M 1468, M 1469, M 1470.

Remarks.—The foregoing description is based on fragments and is therefore to a certain extent subjective. To date no complete specimen has been found.

Biometric Analysis.—Perusal of the plot of the data on whorl height and breadth in Text Fig. 7 indicates some departure from linearity, but this is not of the order as to necessitate the logarithmic transformation. The figure also indicates further support for the identifications of the fragments here made, as deviating specimens would show up by falling outside the path of ontogenetic development.

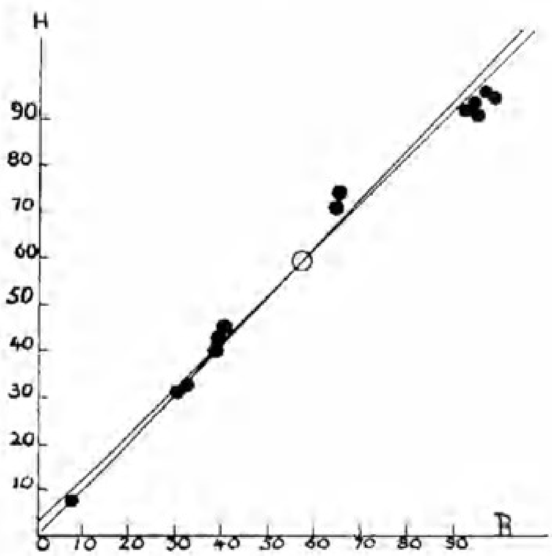

Fig. 7. Covariation of whorl height and whorl breadth for *Myloceras flindersi* (McCoy) with the regression lines. Measurements in mm.

The regression equations are:

$$B = 1 \cdot 02H - 0 \cdot 03$$
$$H = 0 \cdot 97B + 0 \cdot 04,$$

and the correlation coefficient is $r = 0 \cdot 993$, which is highly significant. As shown on the diagram, the regression lines almost coincide.

Myloceras ammonoides (Etheridge)

1909 *Crioceras ammonoides*, Etheridge, p. 502, pl. 30, figs. 8, 9.
1926 *Myloceras ammonoides* (Etheridge fil.), Whitehouse, p. 234, pl. 41, figs. 2a-b.
1926 *Myloceras orbiculus*, Whitehouse, p. 235, pl. 41, figs. 1a-b.

Material.—Two specimens, M 1471, 1472.

Remarks.—The two fragments referred here differ from the closely similar *M. davidi* in their whorl section. This is illustrated graphically in Text Fig. 8, in which the development of length and height of whorl section are compared for the two forms. Comparison with the figures published by Etheridge (1909) and Whitehouse (1926), and the accompanying descriptions, fails to bring forth criteria of sufficient importance as to warrant specific separation of *ammonoides* and *orbiculum*. Thus, both are reported to be compressed, to be more or less ovoid in section, to be densely ribbed with flexed costae that are straight on the venter; only occasional ribs bear tubercles, and the ribs do not bifurcate at the tubercles.

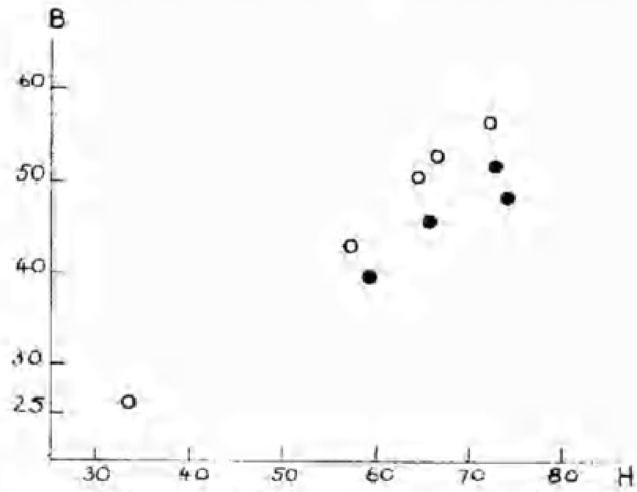

Fig. 8. Development of the whorl section of *Myloceras ammonoides* (Etheridge) and *M. davidi* Whitehouse. The filled dots indicate *ammonoides* and the open dots *davidi*. Measurements in mm.

Myloceras davidi Whitehouse

Pl. 3, fig. 4; pl. 4, figs. 1-4; pl. 5, figs. 3, 4

1909 *Crioceras* sp., Etheridge, p. 144, pl. 38, figs. 1, 2.
1926 *Myloceras davidi*, Whitehouse, p. 235, pl. 37, figs. 2a-c.
1958 *Myloceras davidi* Whitehouse, Glaessner, p. 217, pl. 26, figs. 2-3.

Description.—This species is characterised by the whorl section, compressed and broadest at the dorsolateral shoulders, the numerous thin, sharp, flexed costae, provided with small spinate ventrolateral tubercles and the initial coiling. Many ribs bifurcate at about the middle of the flanks and join up again at the ventrolateral tubercles (Pl. 4, Fig. 3) or two ribs may unite at a tubercle. The ribs swing forwards on the dorsum. On rounding the bend the whorl section becomes more quadrate but thereafter reverts to the usual compressed form. Suture shown in Pl. 4, Fig. 2.

Material.—19 fragments. M 1417, M 1420, M 1473, M 1474, M 1475, M 1476, M 1477, M 1478, M 1479, M 1480, M 1481, M 1482, M 1483, M 1484, M 1485, M 1486, M 1487.

Remarks.—This species is the most richly represented one in the collection. Unfortunately, very few of the fragments permitted measurements. *M. davidi* and *M. ammonoides* are not easy to hold apart, particularly in crushed specimens, as both are compressed and have much the same type of ornament. Moreover, one of the characteristics considered specific for *M. ammonoides,* namely, the bundling of ribs at the ventrolateral tubercle, has been observed to occur in *M. davidi,* together with rib division. In fact, on the basis of the information offered by the present material, it would seem that the whorl section offers the only more or less reliable way of holding the two species apart. The two specimens figured by Glaessner (1957) from New Guinea are typical of the species.

Family ACONECERATIDAE

Genus FALCIFERELLA Casey, 1954

Falciferella reymenti Brunnschweiler?

Pl. 5, Fig. 6

1959 *Falciferella reymenti,* Brunnschweiler, p. 16, pl. 1, figs. 7, 8.

Remarks.—The shell is not preserved on any of these specimens, hence it is not possible to provide observations concerning the ornament. Brunnschweiler (1959, p. 17) noted that whenever any indication of falcoid striation or ribbing is shown it is on the dorsolateral part of the flanks.

Material.—Five fragments. M 1488, M 1489, M 1490, M 1491, M 1492.

Falciferella sp. nov.

Pl. 5, Fig. 5

Remarks.—Several crushed specimens of a *Falciferella* occur in the material. These are of a form, smooth except for faint lateral striae. Unfortunately, the material is insufficient for description.

In addition to these aconeceratids the material also contains several fragments of ammonites possibly referable to the genera *Beudanticeras* and *Sanmartinoceras.*

Material.—Figured specimen. M 1493.

ON THE DISPERSAL OF HETEROMORPHIC AMMONITE SHELLS

Growth of the heteromorphic shell. Changes in the coiling of a cephalopod shell depend on fluctuations in the allometric relations governing growth of the same. For the purpose of simplifying the following discussion it will be taken that growth occurs by means of two centres, one controlling the dorsal part of the shell, and one its ventral part. If the growth rates of the dorsum and venter are equal (isometric growth), a straight shell results (for example, straight nautiloids). In ammonites, however, the growth rate of the venter is usually many times greater than that of the dorsum, and coiled shells with embracing whorls result—the greater the ventral growth rate, the greater will be the degree of involution of the shell. Hence, the position may be summarised by saying that the growth of the venter is always positive allometric with respect to the growth rate of the dorsum, apart from the special case of equality of the growth rates. A heteromorphic shell will result when the two rates of growth fluctuate. Hence, in *Labeceras* the ventral rate of growth is initially slightly greater than the dorsal rate of growth, the difference being so slight, that the whorls are never in contact. This stage is followed by a period of isometric growth, after which a return to much the same growth differences as during earlier ontogeny is made. For *Myloceras* the growth differences are, for about the first whorl, similar to those pertaining in *Labeceras*, after which a period of increase in the positive allometric relationship takes place. Here, the whorls are just in contact with each other. This growth stage is followed by a period of isometric growth, after which a reversion to the earliest pattern occurs.

It is well known that the spiral of the ammonite shell may be described by the logarithmic spiral. That is: $r = ae^{\gamma\omega}$, where a is a constant, r the shell radius, ω the angle of the spiral, and γ is a factor which determines the shape of the curve. The factor γ thus decides whether the shell will be involute, evolute or with the whorls not in contact (Haarländer, 1952). During part of the growth of both *Labeceras* and *Myloceras* the shell describes a logarithmic spiral. However, particularly in connection with the formation of the body chamber this is not so. This is the most important difference between heteromorphic ammonites (excluding those in which the logarithmic spiral is followed at all growth stages – in a sense these are not genuine heteromorphs) and normal ammonites.

The Relationship Between Shell Shape and Shell Dispersal.—In this section the importance of the shape of the shell with respect to nekroplanktonic dispersive possibilities is reviewed and some formulae for the volume of certain idealised shell types given. According to the results obtained by my investigations on factors in the distribution of fossil cephalopods (Reyment, 1958) the orthoconic type of shell is one with excellent floating capabilities; hence, one likely to be widely spread nekroplanktonically. The volume of an idealised orthocone is given by the simple expression: $V = \frac{1}{3}\pi r^2 h$, where r is the radius of the base and h is the height of the shell. In this kind of shell the maximum exposure of surface area is achieved and the maximum relative uplift results. For dead shells the buoyancy is decreased by the weight of the body chamber. It could be shown experimentally (Reyment, 1958, p. 122) that the body chamber of an orthocone must exceed half of the total shell length if a shell is to sink. A rough expression for the mass of the aragonite in a conical shell, assuming a thickness of 1 mm., is $M = 0{\cdot}98\,\pi\,(r^2{}_1 h_1 - r^2{}_2 h_2)$, where r_1 and r_2 are the differences in radius due to wall thickness and h_1 and h_2 are the corresponding differences in height. Similar expressions may be derived for shells of elliptical cross section (the baculitid type).

For coiled shells the effective volume depends on the degree of involution of the shell, the lesser the degree of evolution the greater the effective volume. The effective volume of a coiled evolute shell the whorls of which are just in contact is given by the following expression (kindly derived for me by Dr. I. R. Nystedt, Dept. Mathematics, University of Stockholm):

$$V = \int_{-\pi}^{\omega} a^2 \left(e^{\omega \cot\Omega} - e^{(\omega-2\pi)\cot\Omega}\right)^2 \cdot \pi k \frac{a}{2}\left(e^{\omega\cot\Omega} - e^{(\omega-2\pi)\cot\Omega}\right) d\omega$$
$$- \frac{a^3 k \sin\Omega}{6}\, k_1{}^2 k_2\, R^3$$

where Ω is the tangential angle to the radius, ω the angle of rotation, r the radius. k and a constants, $R = ae^{\omega\cot\Omega}$, $k_1 = 1 - e^{-2\pi\cot\Omega}$, and $k_2 = 1 + e^{-2\pi\cot\Omega}$.

This will also apply to heteromorphic shells as long as the logarithmic spiral is followed. Generally, the combination of the properties of straight shells and evolute shells met with in heteromorphic ammonites, as in *Labeceras* and *Myloceras*, indicates high buoyancy properties, owing to the maximum utilisation of the entire length of the cone in the effective volume. Consequently, it is to be expected that heteromorphic ammonites will be good floaters in the nekroplanktonic state (Reyment, 1958, p. 172), depending naturally on the length of the body chamber. For *Labeceras oodnadattaensis* sp. nov. the body chamber makes up 47 per cent of the total shell length, which is within the bounds required in order for the empty shell to float. In Fig. 9a-b the nekroplanktonic floating positions for *Labeceras* and *Myloceras* are shown.

Fig. 9. a, Floating position for *Labeceras*; b, floating position for *Myloceras*.

Evidence for Nekroplanktonic Dispersal.—This is of two kinds, geographic and sedimentologic. The relatively wide geographic distribution of some of the species treated in this paper is suggestive. Firstly, we have the expected wide distribution of species in the Great Artesian Basin—practically all of the forms among the heteromorphic ammonites treated by Whitehouse (1926) in his monograph also occur in the South Australian material. Secondly, there is the occurrence of these heteromorphs in New Guinea, amongst them the forms recorded by Glaessner (1958), including *Labeceras crassum* Spath and *Myloceras davidi* Whitehouse. Finally, there is the important occurrence of *Labeceras crassum* Spath and *Myloceras axonoides* (Etheridge) in Portuguese East Africa. The buoyant structure of these shells suggests that possibilities of wide-ranging oceanic transport, as has been observed for the shells of *Nautilus* (cf. Reyment, 1958).

The nature of the sediment in which the ammonites occur is of the calcareous tidal mud type, such as that forming in the Bahamas Islands area today (cf. Reyment, 1958), and also in the Jurassic deposits of Solnhofen and Holzmaden, Germany. The drifting shells finally fastened in the shallow water calcareous sediment.

The actual living place of the ammonites was probably in the sea nearby and even further out, but this can, of course, only be a matter of speculation. The only certain fact is that the places of occurrence of the ammonite shells do not represent the area in which they actually lived.

STRATIGRAPHIC CONCLUSIONS

All ammonites are of Albian age and are to be correlated with the *varicosum-equatoriale* zones of the standard English Gault succession (Spath, 1925), and possibly the *orbignyi* zone (Whitehouse, 1926).

ACKNOWLEDGMENTS

The author wishes to express his sincere thanks to Geosurveys of Australia and the Department of Mines of South Australia for supplying all of the study material. Particular thanks for assistance in many ways are due to Dr. R. Brunnschweiler, formerly of Geosurveys of Australia, Dr. N. Ludbrook and Dr. H. Wopfner of the Geological Survey of South Australia. Dr. Ludbrook also kindly arranged publication of these results. The photographs were taken by Mr. L. Kutnar, formerly of the Department of Geology, University of Stockholm. In connection herewith Mr. Kutnar devised a way of photographing plasticene casts of ammonites.*

* All ammonites were coated with ammonium chloride prior to photographing. It is, however, not possible to achieve a smooth distribution of this substance on plasticene casts of whorls, which usually means that the cast must be photographed without preparation. Mr. Kutnar found that by first chilling the cast and then spraying with an acrylate fixing base (Zapon plastic lacquer—used for fixing pencil drawings) a surface could be produced on which the ammonium chloride will fasten satisfactorily.

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EXPLANATION OF PLATES

PLATE 1

Fig. 1. *Labeceras (Labeceras) laqueum* (Etheridge). View of part of the shaft and the crook and the last six sutures (observe the crowding of the final two sutures). M 1439, X1.

Fig. 2. *Labeceras (Labeceras) crassum* Spath. Portion of the body chamber. M 1440, X1·8.

Fig. 3. *Labeceras (Labeceras) compressum* Whitehouse. An entire body chamber, running from the final suture to the apertural lappets. Fragments of shell material of the same species attached. This specimen retains largely its (altered) shell material. M 1441, X1·4.

Fig. 4. The same species. Ventral view showing the sutures. M 1415, X2·1.

Fig. 5. *Labeceras (Labeceras) oodnadattaensis* sp. nov. Lateral view of the holotype showing several of the final sutures. S.A.M., M 1444, X1·2.

Fig. 6. *Labeceras (Appurdiceras) cordycepoides* (Etheridge). Lateral view of a fragment showing three sutures. M 1446, X1·3.

Fig. 7. Same species. A body chamber. M 1447, X1·3.

Fig. 8. *Myloceras intermedium* (Whitehouse). Part of a body chamber. M 1459, X1.

PLATE 2

Fig. 1. *Myloceras nautiloides* (Etheridge). Ventral view of part of a body chamber. M 1448, X1.

Fig. 2. Same species. Lateral view of septate whorls. M 1450, X1·3.

Fig. 3. *Myloceras plectoides* (Whitehouse). Early septate part of a shell. M 1451, X1·2.

Fig. 4. *Myloceras buccatum* (Whitehouse). Part of the body chamber and the last three sutures. M 1458, X0·6.

PLATE 3

Fig. 1. *Myloceras axonoides* (Etheridge). Lateral aspect of part of an inner whorl. M 1460, X1·5.

Fig. 2. *Myloceras flindersi* (McCoy). Crushed fragment showing the swung ribbing. M 1465, X1·6.

Fig. 3. Same species. M 1469, X0·5.

Fig. 4. *Myloceras davidi* Whitehouse. Specimen showing part of an early whorl. M 1486, X1.

PLATE 4

Fig. 1. *Myloceras davidi* Whitehouse. Impression. M 1473, X1·3.

Fig. 2. Same species. Cast showing the suture line. M 1417, X1·1.

Fig. 3. Same species. Crushed cast showing flexed ribs and the nature of the tuberculation. M 1474, X1·1.

Fig. 4. Same species. M 1481, X1·3.

PLATE 5

Fig. 1. *Myloceras plectoides* (Etheridge). Specimen showing sutures. M 1419.

Fig. 2. Same species. Plasticene mould of a specimen. M 1457, X1.

Fig. 3. *Myloceras davidi* Whitehouse. Plasticene mould of a specimen. M 1485, X1·2.

Fig. 4. Same species. Internal structure of chambers. M 1487, X1.

Fig. 5. *Falciferella* sp. Crushed specimen in the body chamber of a *Myloceras*. M 1493, X2.

Fig. 6. *Falciferella reymenti* Brunnschweiler? Specimen showing the development of the inner whorls. M 1488, X6.