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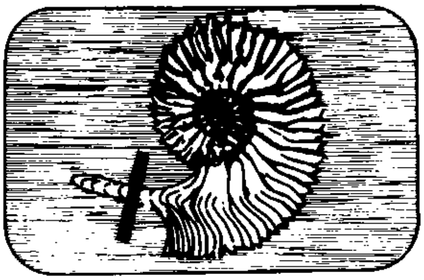
Article abstract

Certain pairs of ammonite "species", different in size and exhibiting contrasting morphology on their adult stages, are shown to possess inner whorls (earlier growth stages) which are almost identical in all morphological aspects. The similarities indicate close genetic relationship, the divergence in size and adult body chamber being secondary sexual characters. Five such dimorphic pairs occur together in the same strata in the Middle Jurassic Yakoun Formation on the Queen Charlotte Islands and It is suggested that they represent the two sexes.



Sexual Dimorphism in Jurassic Ammonites from the Queen Charlotte Islands

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Summary
Certain pairs of ammonite "species", different in size and exhibiting contrasting morphology on their adult stages, are shown to possess inner whorls (earlier growth stages) which are almost identical in all morphological aspects. The similarities indicate close genetic relationship, the divergence in size and adult body chamber being secondary sexual characters. Five such dimorphic pairs occur together in the same strata in the Middle Jurassic Yakoun Formation on the Queen Charlotte Islands and it is suggested that they represent the two sexes.

Introduction

Nowhere in the stratigraphic record have such precise faunal zones been established as in the Jurassic of North-western Europe where this period (with a duration of some 40 to 56 million years) has been subdivided into more than 50 zones based on the succession of ammonite faunas. This succession can be closely matched on all continents even though endemism and the fluctuating developments of faunal realms sometimes make this difficult. Careful analysis of ammonite faunas allows subzones of even shorter duration to be recognized.

A number of paleontologists in the past noted the occurrence together in the same bed of two forms of ammonites which, though differing greatly in size, ornamentation and apertural modifications at the adult stage, had inner whorls (i.e., the immature phragmocone) which were virtually indistinguishable. Usually these adult forms were classified as different species, genera or even families, and yet incomplete specimens could not confidently be separated. This dimorphism is now recognized in an increasing number of ammonite faunas and is believed to be sexual in origin.

In the last decade a renewed interest in the occurrence of dimorphism in ammonites has led to considerable changes in classification and understanding of these extinct organisms. While the occurrence of dimorphism in ammonites, and its possible sexual origin, has long been known, the present revival of interest stems largely from the work of Makowski and Callomon who, in 1963, simultaneously and independently published major reviews on this subject. The recognition of dimorphism in several Bajocian (Middle Jurassic) ammonite faunas from the Yakoun Formation on the Queen Charlotte Islands has permitted revision and simplification of the biological classification of these forms. As has often been the case elsewhere, several of the forms now regarded as sexual dimorphs belonging to the one biological species had been classified previously as different genera and even different families because of their widely different morphologies.

How, then, do paleontologists recognize two groups of ammonites as the corresponding members of a dimorphic species? To discuss this problem we must first understand the nature of growth of the ammonite shell and the signs establishing maturity.

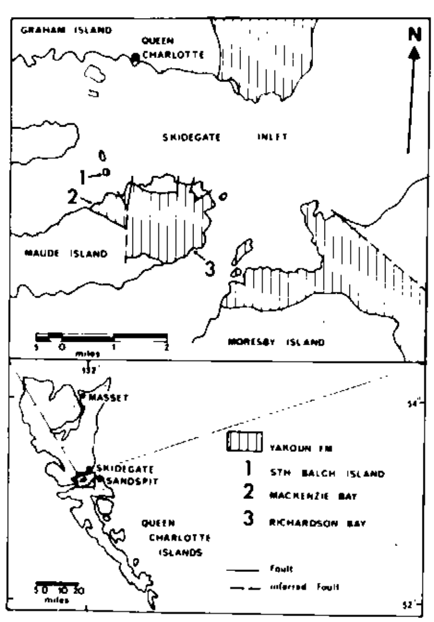
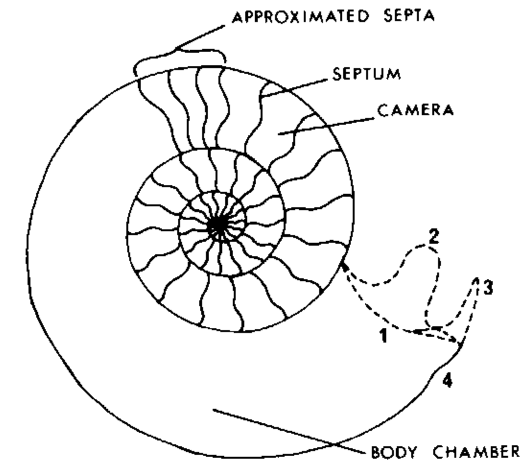
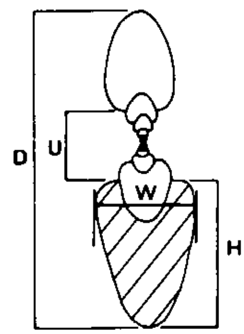


Figure 1
Map of part of Skidegate Inlet, Queen Charlotte Islands, showing localities at which Middle Jurassic ammonites discussed in this article were collected.

Growth of the Shell. Following the initial whorl, which probably represents the larval stage, the ammonite shell generally follows a logarithmic spiral. Growth is accretionary, but does not continue until the animal dies; maturity is reached at a definite, pre-determined size. Prior to this point growth slows down and finally stops.

Features of the Mature Shell. (a) As the growth rate decelerates, the camerae being sealed off become shorter and so just before growth ceases the septa are more closely spaced and said to be approximated (Fig. 2). The complexity of folding of the septal edges is often simplified at this stage. (b) The last part of the shell which is occupied by the adult animal (body chamber) usually deviates from the logarithmic spiral, becoming more or less "uncoiled" and following a somewhat elliptical spiral. (c) The aperture of the body chamber (peristome) is usually modified in a number of ways (Fig. 2). Preceding the peristome there is frequently a constriction in the shell, followed by a flared, smooth collar and lip. On others long, spatulate extensions of the shell occur either in the lateral position (lappets) or in the ventral position (rostrum). (d) The external ornamentation of the shell of





1 SIMPLE APERTURE
2 LAPPET
3 ROSTRUM
4 CONSTRICTION

Figure 2
Median section (left) of ammonite shell showing major features referred to in text, with four of the possible modifications which may occur at the adult aperture.

Cross-section (right) indicates positions at which shell parameters were measured for the shaded whorl: D = shell diameter; U = umbilical diameter; W = width of whorl; H = height of whorl.

the body chamber is often strongly modified compared to that on the earlier whorls (phragmocone). This may involve the loss of previously strong ornamentation, appearance of new features, increase or decrease in the density and strength of spines and ribs.

Establishment of a Dimorphic Relationship

Several pre-requisite conditions are now commonly accepted as having to be fulfilled before two ammonite groups are designated as a dimorphic "pair" (see Makowski, 1963; Callomon, 1963).

(a) Since in establishing two groups of ammonites as sexual dimorphs we are recognizing that they are the male and female forms of a single biological species, it is necessary to show strong genetic similarities between them. This is established by the strong similarities in the morphology of the phragmocone whorls; changes in morphological features during growth should be seen in both forms. Changes occurring on the body chamber and the differences in maximum diameter of the adults are regarded as secondary sexual characteristics. A similar history of evolutionary development (phylogeny) should also be seen in both forms, with new features appearing concurrently in each "lineage".

(b) Intermediate forms connecting the two dimorphs should be lacking; such forms would indicate all were part of a single, interbreeding population showing great morphological diversity. This applies especially to size differences; Makowski (1963) established a clear break in the number of complete whorls (his "morphological hiatus") in the large (macroconch) and small (microconch) members of a dimorphic pair.

(c) Both forms are expected to occur in the same strata. This is an idealized condition which, though usually fulfilled, is not regarded as being as important as (a) or (b). Apart from the subjectivity of the term "same strata" (due to variations in sedimentation rates and/or faunal abundance) there are several factors which may influence geographical distribution of the members of a dimorphic pair. Due to pronounced differences in size and ornamentation of adult animals they may well have occupied different ecological niches, and migration and breeding behaviour may have been different in the two sexes (see (d) below).

(d) The numerical ratio of the two sexes should be comparable to that found in living species (and is generally assumed to be 1:1). Many ammonite faunas are recorded, however, in which one dimorphic form is predominant. Different ecological adaptations and breeding behaviour may again explain these divergences. Knowledge of the migratory habits of the two sexes in various Recent cephalopod species, in which segregated schools move separately to shallow water for breeding, has been summarized by Westermann (1969, p. 19 and 20). Also large, smooth shells and smaller shells with heavy ornamentation would be expected to have different potentialities for fossilization. Collection failure is yet another factor affecting the ratio of sexes. Other post-mortem factors affecting this ratio have been discussed by Westermann (1964, p. 36 and 37).

Examples of Dimorphism in British Columbia Ammonites

Middle Bajocian ammonites from the lower part of the Yakoun Formation exposed along the shores of Skidegate Inlet in the Queen Charlotte Islands include species from two families (Stephanoceratidae, Sphaeroceratidae) which exhibit very different forms of dimorphism (Fig. 1 and Table I). The low diversity of these faunas and their occurrence at restricted stratigraphic levels in thick sequences of volcanically derived sandstones, shales and agglomerates have made it possible to recognize dimorphic pairs at the species level. There is still considerable discussion among paleontologists as to how a recognized dimorphic pair should be named, especially since most species are already named and have often been placed in quite different taxa (genera or families). Because only single species of a few distinctive genera are known from the lower Yakoun Formation, and because the morphological criteria agree so well, the two members of each dimorphic pair are here given the same species

Table I *Faunal Distribution*

	Richardson Bay	MacKenzie Bay	South Balch Island
Zemistephanus richardsoni ♀	—	18	—
Zemistephanus richardsoni ♂	—	5	—
Stephanoceras itinsae ♀	—	—	31
Stephanoceras itinsae ♂	—	—	7
Stephanoceras skidegatense ♀	12	—	—
Stephanoceras skidegatense ♂	8	—	—
Chondroceras defontii ♀	8	—	—
Chondroceras defontii ♂	2	—	—
Chondroceras oblatum ♀	—	—	8
Chondroceras oblatum ♂	—	—	3

name. The large number of taxa previously used in describing these faunas (Whiteaves, 1876; McLearn, 1927, 1929, 1930) is considerably reduced and phylogenetic relations clarified.

Family STEPHANOCERATIDAE
Neumayr, 1875
Genus *Stephanoceras*
Waagen, 1869

From the outcrop on South Balch Island two ammonite forms, very different in size, have been collected (Fig. 3). They were previously described as two species belonging

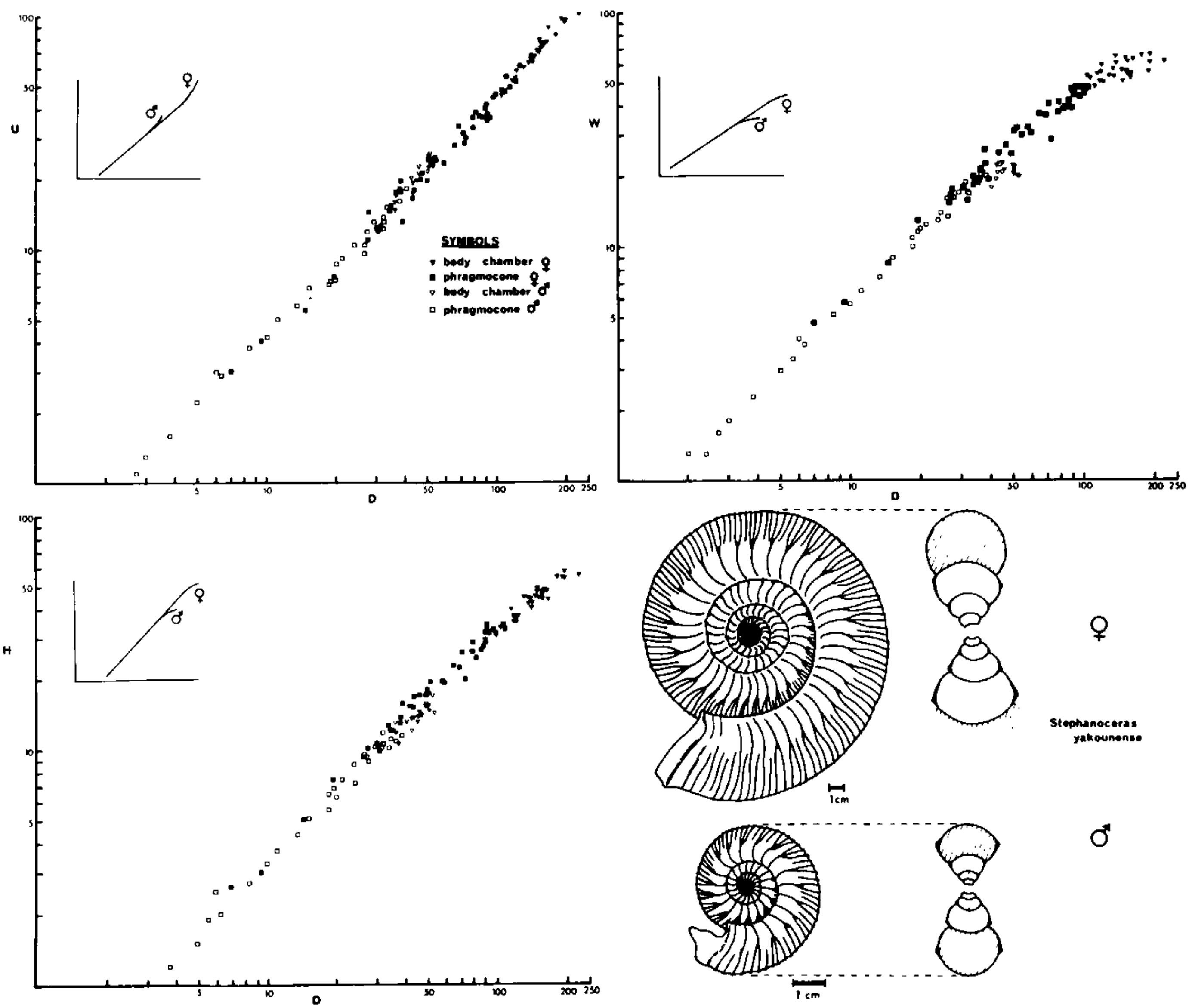


Figure 3
Stephanoceras itinsae ♀, ♂. Plots on double logarithmic scale of shell diameter (D) against umbilical diameter (U), whorl width (W) and whorl height (H); small axes show general correspondence of males and females. Based on measurements from 18 female and 8 male specimens from South Balch Island in Skidegate Inlet. Sketches show general external morphology and cross-sectional shape of both sexes.

to different genera and were placed in different families: *Stephanoceras yakounense* McLearn, 1930 (Family Stephanoceratidae) and *Itinsaites itinsae* McLearn, 1927 (later included in the genus *Normannites* and the family Otoitidae). The large macroconch (conventionally taken to be the female of the species), *S. yakounense*, reaches diameters of 16 to 20 cm and is approximately four to five times the size of the microconch, *I. itinsae*. Throughout the phragmocone both forms exhibit identical morphology in the pattern and density of ribbing, shape of the whorl cross-section, width and height of the whorls, diameter of the umbilicus and suture pattern. Uncoiling in both forms commences at the beginning of the body chamber which becomes more rounded in cross-section and relatively higher than the earlier whorls. It is on the body chamber that differences in ornamentation become apparent: the primary ribs and nodes on the macroconch become very faint and the density of secondary ribs decreases while on the microconch ribbing and nodes remain strong and there is little change in their density. The macroconch shell terminates simply with a smooth, expanded lip while that of the microconch is extended into two long, lateral lappets. The morphology of these two forms is compared in Figure 3 and they are now designated *Stephanoceras itinsae* (McLearn) ♀, ♂.

Similar dimorphism can be shown in another member of this genus, *Stephanoceras skidegatense* (Whiteaves), found at Richardson Bay.

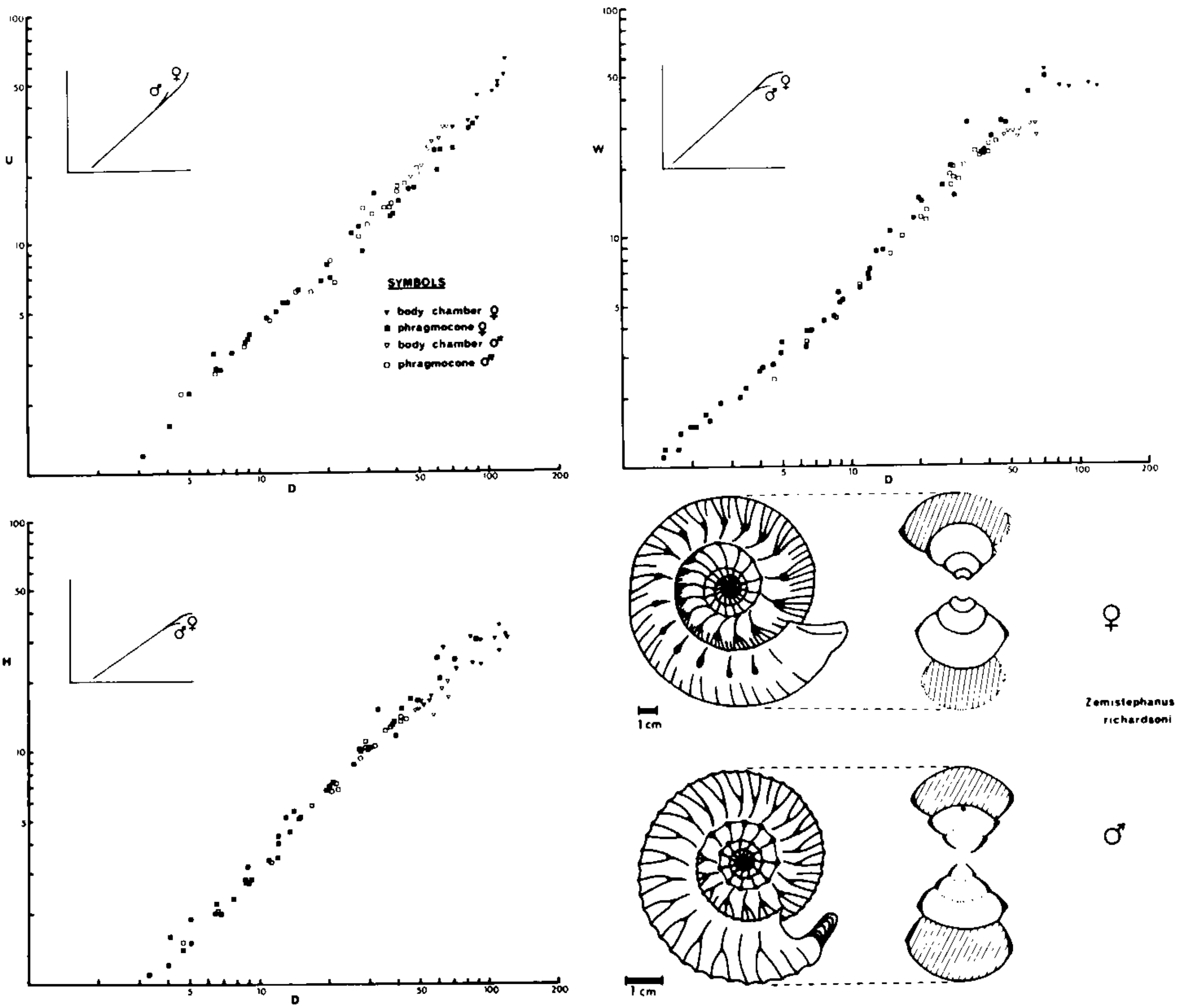


Figure 4
Zemistephanus richardsoni ♀, ♂. *Plots on double logarithmic scale of shell diameter (D) against umbilical diameter (U), whorl width (W) and whorl height (H); small axes show general correspondence of males and females. Based on measurements from 12 female and 5 male specimens from MacKenzie Bay, Maude Island. Sketches show general external morphology and cross-sectional shape of both sexes.*

Genus *Zemistephanus* McLearn, 1927
This genus is known only from southern Alaska (Imlay, 1964) and the Queen Charlotte Islands (McLearn, 1929) and is apparently endemic to western North America. McLearn (1927) erected a new genus, *Kanastephanus,* for some small specimens from the MacKenzie Bay outcrop; it is here suggested that this genus is the microconch form of *Zemistephanus* which comes from the same locality. A previously undescribed species of *Kanastephanus* can be matched at the species level with *Z. richardsoni* (Whiteaves). Both occur in the MacKenzie Bay strata, the macro-conch being twice the size of the microconch. The aperture of the macroconch is simple with a flared, smooth lip while that on the micro-conch is not flared but extended into two short, ventro-lateral lappets. Ribs and nodes on the body chamber of the microconch remain coarse but the shell of the macroconch becomes almost smooth, retaining only rounded nodes on the flanks. In both forms the body chamber uncoils, with rounding of the whorl cross-section and a decrease in its relative width. Dimensions of the inner whorls (width, height and umbilical diameter), shape of the whorl cross-section and ornamentation are the same in both forms (Fig. 4) and undergo similar changes during growth. For instance, in both forms the density of ribbing on the earliest whorls decreases from 8 to 12 on each half whorl to a minimum of 6 to 8 at umbilical diameters between 5 and 15 mm; throughout later growth stages this trend is reversed with an increase to 8 to 12 at the end of the phragmocone.

Famliy SPHAEROCERATIDAE Buckman, 1920
Genus *Chondroceras* Mascke, 1907
Two species of this genus are recognized from the lower Yakoun Formation: *C. oblatum* (Whiteaves, 1876) from South Balch Island and *C. defontii* (McLearn, 1927) from Richardson Bay. These and several other species were originally described under the generic name

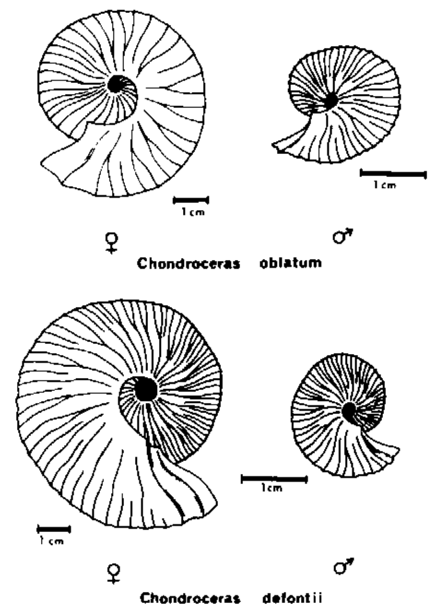


Figure 5
Sketches showing general morphology of dimorphic pairs in (top) Chondroceras oblatum from South Balch Island in Skidegate Inlet; and (bottom) Chondroceras defontii from Richardson Bay, Maude Island.

Defonticeras by McLearn. Tiny microconch specimens, only about two cm in diameter and one-third the size of the macroconch, have now been found by me at these localities. Dimorphism is not as strong as that described above for the two genera of the family Stephanoceratidae. The apertural modifications, whorl dimensions and ornamentation on both phragmocone and body chamber are identical, the only difference being that of adult size (Fig. 5).

Conclusion
The recognition of sexual dimorphism in ammonites allows better under-standing of the biological affinities of forms which previously, on the basis of the very different morphology of the adult shell, have been allied with quite different taxa. A better idea of the evolutionary history of various ammonite families and refined stratigraphic zonation should result as more dimorphic relationships are recognized.

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