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Evolutionary Trends Within Gastroplitan Ammonoids

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ABSTRACT

Middle Albian *Gastroplites* descended from cosmopolitan *Beudanticeras*-like ammonites (*Cleoniceras*) and developed local genera such as the Upper Albian *Neogastroplites* and the Lower Cenomanian *Irenicoceras*. Relationships are postulated with allied genera such as *Lemuroceras*, *Subarctoplites*, *Freboldiceras*, *Tetrahoplitoides*, *Metasigaloceras*, and some members of the *Acanthoceratidae*. Extreme pliability within Gastroplitan morphology permitted adaptation throughout varying palaeoecological regimes.

GASTROPLITES and *Neogastroplites* form a local race of ammonites in Western Canada. Unfortunately, their ancestry is obscured by an excess of taxonomy. The writers consider that the immediate ancestor of the late Middle Albian *Gastroplites* McLearn is a strongly ribbed member of *Cleoniceras* Parona and Bonarelli midway between *Subarctoplites* Casey and *Cleoniceras* s.s.

But the type species of *Subarctoplites* is *Lemuroceras belli* McLearn which is included by Crickmay (4) under his genus *Coloboceras* (*non* Troeussart, 1889, an arachnid) which is an invalid homonym and which has been replaced by *Tetrahoplitoides* Casey (2). The latter has as its type species *Sonneratia stantoni* Anderson which Imlay and Reeside (6, p. 237) suggest to be representative of *Gastroplites*. Other Western Canadian species assigned to *Lemuroceras* by McLearn are variously placed by the writers as follows: viz. *Lemuroceras mcconnelli* (Whiteaves) is a *Subarctoplites* very close to a species of *Cleoniceras*; the latter shows a marked affinity to small specimens of *Beudanticeras glabrum* (Whiteaves) which lack the interruptions of growth (see 13, Pl. 30, Fig. 1). *Lemuroceras irenense* McLearn may well belong to Imlay's new genus *Freboldiceras* but the latter shows a slightly more reduced suture than the former. The form figured by McLearn (9, Pl. V, Fig. 4) as *Lemuroceras* cf. *indicum* Spath is undoubtedly a species of *Arctoplites* Spath.

Certain of the forms referred to *Gastroplites* by Warren (13, Pl. 29, Figs. 8, 9, 11) may be assigned to *Pseudosonneratia* Spath and another (Pl. 29, Fig. 10) to a large, probably new, species of *Subarctoplites*. The specimen questionably referred to *Pusozia* by Warren (Pl. 29, Figs. 6, 7) may be referred to *Uhligella* as it has the same simplified suture. The form *Placenticeras liardense* Whiteaves is placed with *Gastroplites*.

As Casey (2) points out, *Lemuroceras* Spath does not occur in the boreal sphere but there is little question in the writers' minds that Indian *Lemuroceras* are a southern offshoot of the *Cleoniceras* stock that also gave rise to the northern *Subarctoplites*, the Pacific *Tetrahoplitoides*, and probably the Russian *Cymahoplites*.

In searching for an ancestor for *Gastroplites* certain ontogenetic features of that genus are critical: firstly, the innermost whorls are smooth and obese and reminiscent of *Desmoceras*; secondly, the introduction of ribs is lateral,

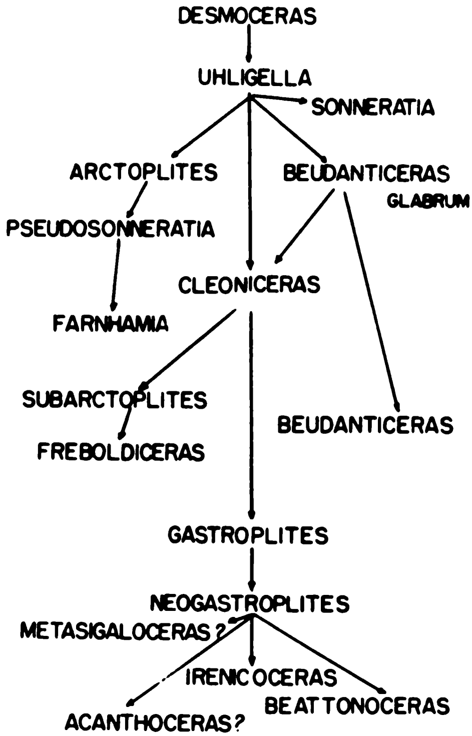


PLATE I: PHYLOGENY OF GASTROPLITAN AMMONOIDS

springing from the umbilical margin by growth line bundling and not crossing the rounded venter; thirdly the ribs are tangential at the umbilical margin at maturity and have such a feature in the early stages. All these nepionic and neanic features are Cleoniceratid.

Cleoniceras is cosmopolitan and is believed to be the ancestral stock for several ammonite lineages which became isolated in Middle Albian time. The Middle Albian ammonite stock known from Alberta contains *Cleoniceras*, *Beudanticeras*, *Subarctoplites*, *Freboldiceras*(?), and *Gastroplites*. But the Middle Albian sea in Alberta is known to have invaded from the Arctic and the southern shoreline of this sea is contained within northeastern British Columbia and central Alberta. It is necessary to seek a boreal ammonite stock to provide the immediate ancestor to both *Subarctoplites* and *Gastroplites*.

From the Arctic realm of continental Canada in the collections of the

University of Alberta there are Lower and Middle Albian specimens assignable to *Desmoceras*, *Uhligella*, *Wollemanniceras*, *Sonneratia*, *Pseudosonneratia*, *Arctoplites*, *Farnhamia*, *Subarctoplites*, *Beudanticeras*, and *Cleoniceras*. Canadian forms that are morphologically similar to *Subarctoplites* such as *Tetrahoplitoides* and *Cymahoplites* are recorded only from the Pacific realm (Queen Charlotte Islands).

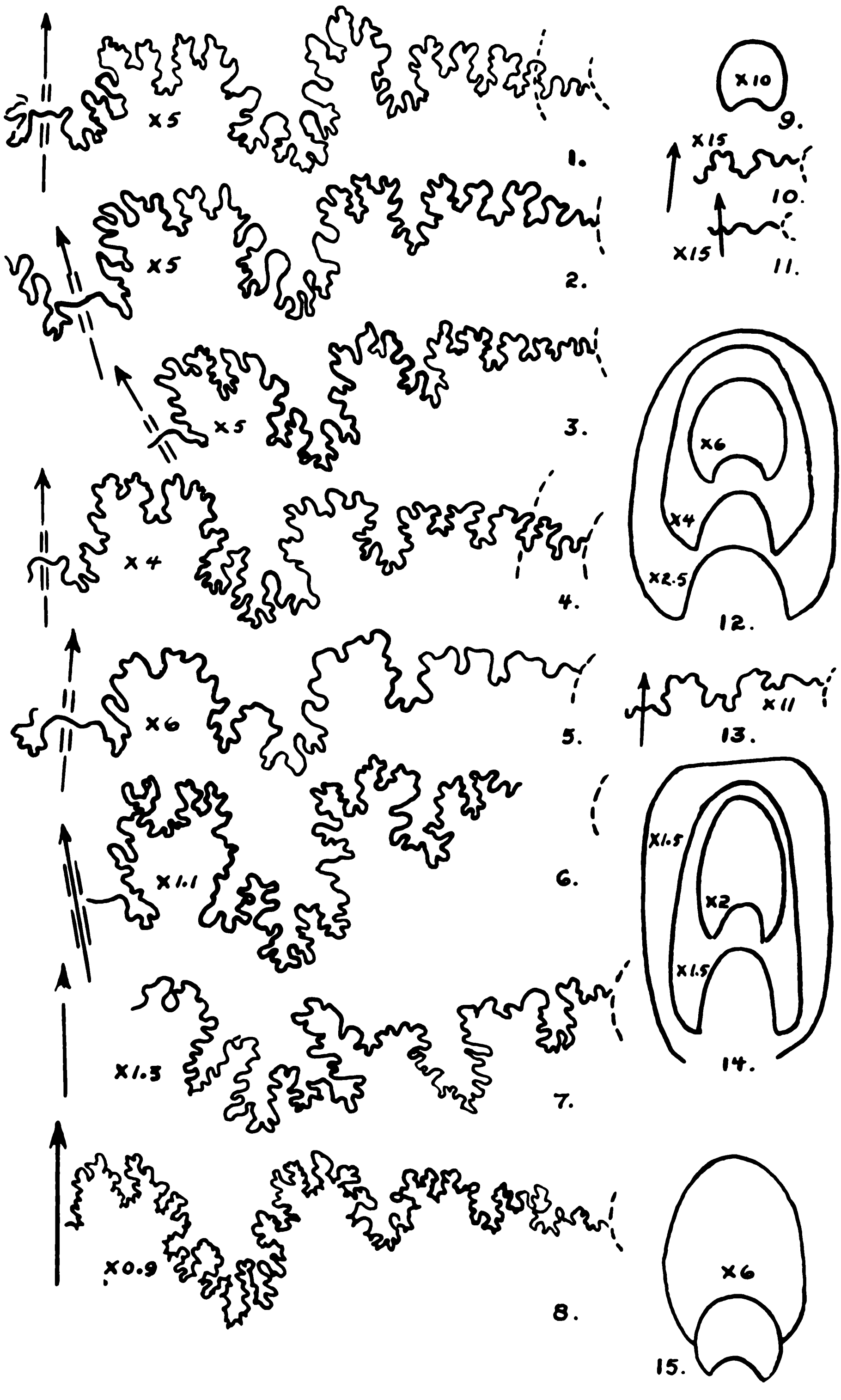
A recent paper by Imlay (5) on Alaskan forms implies an admixture there of both Pacific Ocean and Peace River (Alberta and northeastern British Columbia) elements. The genera common to the Peace River area and Alaska are: *Beudanticeras*, *Cleoniceras*, *Freboldiceras*, *Subarctoplites*, and "*Gastroplites*." Of the above, *Beudanticeras* and *Cleoniceras* are widespread but an anomaly appears in that, in Alaska, *Cleoniceras* comes both below and above "*Gastroplites*" whereas in the Peace River area *Cleoniceras* comes below *Gastroplites* and they are not found together. There is, however, a near-homeomorph of *Gastroplites kingi* McLearn from the lower Mackenzie River area which has a more complex suture and a different ontogenetic development which might properly belong within the stratigraphic range of *Cleoniceras*. The writers recognize as yet only one species of *Gastroplites* from the Canadian Arctic slope and that is a form very close to *Gastroplites liardense* (Whiteaves) which we consider Upper Albian in age.

Examination of the above lists shows that of the forms so far collected only *Cleoniceras* has the shell morphology to provide the inner whorls of both *Subarctoplites* and *Gastroplites*.

An examination of the sutures (see Plate II) of *Beudanticeras* aff. *B. glabrum* (Fig. 3), *Subarctoplites mcconnelli* (Fig. 2), *Subarctoplites*(?) sp. (close to *Cleoniceras*) (Fig. 1), and *Subarctoplites belli* (Fig. 4) shows a common similarity to the *Cleoniceras devisense* Spath suture illustrated by Spath (10, Pl. 4, Fig. 7) from the lower Gault. The suture of *Gastroplites* (Fig. 5) shows a simplification but no reduction in elements of suture compared to the *Cleoniceras–Subarctoplites* pattern. The suture of *Neogastroplites cornutus* (Whiteaves) (Fig. 6) from the Upper Albian shows the restoration of the earlier complexity to the suture without much modification from the *Cleoniceras–Subarctoplites* line although the suture of the inner whorls of *Neogastroplites* passes through the simplified *Gastroplites* stage.

The suture of *Neogastroplites septimus* Warren and Stelck from the Lower Cenomanian (Fig. 7) has a lower profile but corresponds fairly well to the Upper Albian pattern. The suture of *Beattonoceras ontkoi* Warren and Stelck (Fig. 8) mimics the Upper Albian *Neogastroplites* sutures except for the extent of the ventral lobe itself which is not very well known. *Irenicoceras* Warren and Stelck has a suture that reflects the lowered profile of the Cenomanian *Neogastroplites* although matching in pattern the Albian *Neogastroplites*. If sutures show genetic relationships, the *Gastroplites* stock from *Cleoniceras* to *Beattonoceras* is monophyletic.

Whorl sections of *Gastroplites* (Figs. 14 and 15) show a progressive flattening of the sides and venter with growth and for illustration we have


X5
1.
X10
9.
X15
10.
X15
11.
X5
2.
X5
3.
X6
X4
X2.5
12.
X4
4.
X6
5.
X11
13.
X1.1
6.
X1.5
X2
X1.5
14.
X1.3
7.
X0.9
8.
X6
15.

selected a species that delays this ventral flattening until a late stage. In *Subarctoplites* (Figs. 9 and 12) the conch follows through to a subquadrate section in maturity but never loses the rounding of the venter. However, in some *Gastroplites* as in some *Cleoniceras* there are mature species with a smooth ultimate whorl and in these the venter once again becomes rounded and this stage gives a homeomorph of *Beudanticeras*. Smooth *Neogastroplites* can usually be distinguished from *Beudanticeras* by the retention of the rostrum on the aperture but the smooth *Beattonoceras* is easily mistaken for *Beudanticeras*. We also have in our collections *Gastroplites* that are near-homeomorphs of *Cymahoplites*.

The writers have found considerable difficulty in making generic references because of homeomorphy in ribbing patterns in the adult stage of different lineages. In sharp contrast to this problem of convergence we are faced with intraspecific variation. The late J. B. Reeside, Jr. (personal communication), while studying *Neogastroplites* found multiple heteromorphic series within each of several species of that genus. Such pliability of form is also suggested in some measure for the genus *Gastroplites*, as many "species" may be collected from a single nodule. In earlier beds, species of *Subarctoplites* may be found showing a varied delay in the introduction of ribbing. Warren (13, Pl. 30, Figs. 3 and 4) figured a "*Beudanticeras*" *glabrum* showing *Cleoniceras*-like ribbing on one side, but this feature is lacking on the other side of the same specimen.

Similarly *Gastroplites* shows variation of involution, as the width of the umbilicus in *Gastroplites allani* McLearn is one-sixth of the diameter,

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PLATE II: GASTROPLITAN SUTURES AND WHORL SECTIONS

FIG. 1. *Subarctoplites* sp. (×5) ct. 1159 a, U. of A. external suture at whorl height 13 mm., from specimen showing late introduction of ribbing after diameter of 25 mm. from Loon River formation, Peace River, Alberta. FIG. 2. *Subarctoplites* cf. *S. mcconnelli* (Whiteaves) (×5) ct. 1159 b, U. of A. mirror image of external suture at whorl height 12 mm. from specimen showing early introduction of ribbing before 4 mm. diameter, from same nodule as above. FIG. 3. *Beudanticeras* cf. *B. glabrum* (Whiteaves) (×5) ct. 1159 c, U. of A. external suture at whorl height 14 mm. from unribbed specimen, from same nodule as above. FIGS. 4, 9–12. *Subarctoplites belli* McLearn from upper part of Loon River formation, Peace River, Alberta; 4, ct. 1160 a, U. of A. mirror image of external suture at whorl height 15 mm. (×4); 9, ct. 1160 b, U. of A. whorl section (×10) at 1 mm. height; 10, 11, external suture of same (×15) at whorl height 1 mm. and 0.4 mm.; 12, ct. 1160 a, U. of A., whorl sections at heights 2.5 mm., 7 mm., 16 mm. (×6, ×4, ×2.5) respectively. FIGS. 5, 13–15. *Gastroplites* sp. Cadotte sandstone, near Gates on Peace River, British Columbia, ct. 1161 U. of A.; 5, external suture at whorl height 10 mm. (×6); 13, external suture at whorl height 1.9 mm. (×11); 14, whorl sections at height 9 mm., 22 mm., 26 mm. (×2.0, ×1.5, ×1.5); 15, whorl sections at heights 1.7 mm. and 3.9 mm. (×6). FIG. 6. *Neogastroplites cornutus* (Whiteaves) external suture at whorl height 58 mm. (×1.1) after McLearn, 1933, Plate 4, St. John Shale, below fish scales, Peace River, British Columbia. FIG. 7. *Neogastroplites septimus*, Warren and Stelck, ct. 1134 U. of A., external suture at whorl height 75 mm. (×1.3) St. John shale, above fish scales, Peace River, British Columbia. FIG. 8. *Beattonoceras ontkoi* Warren and Stelck, ct. 1131, U. of A., external suture at whorl height 85 mm. (×0.9), St. John shale above the fish scale sand, Peace River, British Columbia.

whereas, in *Gastroplites anguinis* McLearn it is one-third. The same range may be noted within forms assigned to one species viz. *Castroplites canadensis* (Whiteaves). *Gastroplites anguinis* has about the same involution as *Lemuroceras* whereas *Gastroplites allani* has about the same involution as *Subarctoplites*. In our opinion, this variability is an expression of their potential adaptability to varying ecological conditions. This may well be the reason why *Gastroplites* stock was the only ammonite lineage to maintain itself from the Middle Albian to Lower Cenomanian stage in the Peace River area of Western Canada.

The history of the late Albian seaways in Western Canada has been treated previously by the junior author (12). In brief, the early Albian boreal sea was confined to the Arctic slope but an embayment developed which reached as far south as central Alberta by Middle Albian time. This embayment was separated from the Pacific Ocean by the land mass of Cordilleran British Columbia and the Yukon and a cosmopolitan aspect pertains only to the Lower Albian forms and not to those of the Middle Albian. No Middle Albian species of ammonites is common to both the interior embayment and the Pacific coast. By Upper Albian time the south end of the Arctic embayment became a landlocked sea (Mowry) that covered most of northeastern British Columbia, Alberta, southern Saskatchewan, eastern Montana, the Dakotas, Wyoming, Nebraska, and possibly Colorado.

As far as can be determined the boreal link was broken during the development of *Gastroplites*. It was established briefly in *Gastroplites liardense* time, as *Gastroplites* appeared briefly in northern Yukon (and Alaska?) and reached England. For the remainder of Upper Albian time it was an interior sea and in the Cenomanian finally connected with the southern flooding from the Gulf of Mexico. The Gastroplitan stock of ammonites disappeared when the waters regained oceanic coalescence in Upper Cenomanian time.

It is questionable whether a lineage as vigorous as the *Gastroplites* stock could easily be extinguished. It persisted through varying salinities, and from open sea to euxinic and landlocked basinal conditions, and maintained itself during intermittent connections with Arctic, Gulfian, and perhaps Atlantic waters. During the period of transition from Lower to Upper Cretaceous, the *Neogastroplites* group of ammonites developed a wide variety in form, size, and ornament. Their size is known to range from about half-an-inch in diameter to large discs measuring eighteen inches across. The shape of whorl section ranges from globose to lenticular with some quadrate forms. Ornament ranges from ribbed to smooth, bullate and clavate forms, and forms with and without siphonal nodes.

Such a multiplicity of morphologic characters is apt to give rise to a corresponding multiplicity of discrete lineages, if stabilized. The writers suggest that many of the "orphan" genera of late Cenomanian time may have a vigorous parentage within *Neogastroplites* s.l. Certain forms like *Metasigaloceras*(?) (Hyatt) figured by Warren and Stelck (14) from the

Lower Cenomanian of northeastern British Columbia could be congeneric or at least ancestral to that genus. The species they figure has definite connection with *Neogastroplites*. Cenomanian *Neogastroplites* tend to have simple ribs on the outer whorl although branching ribs appear on the inner whorls. This gives the conch an appearance of an involute *Acanthoceras*.

The ancestry of the family Acanthoceratidae which has been attributed to *Lyelliceras* could as easily be attributed to an evolute *Neogastroplites*. *Lyelliceras* carries alternate and not opposite lateroventral nodes. Since *Neogastroplites* often carries siphonal nodes we feel that it represents a more logical ancestor for many of the Acanthoceratids.

The external homeomorphy of *Gastroplites liardense* to genera like *Irenicoceras*, *Stoliczkaia*, *Utaturiceras*, and *Metoicoceras* is obvious. The relationship of these to *Neogastroplites* is not as obvious but may be more pertinent. Such North American genera as *Budaiceras* and even *Dunveganoceras* may have an origin in evolute Neogastroplitids. *Acanthoceras athabascense* Warren and Stelck may have the same heritage. The writers have long speculated that *Ammonites glossonotus* Seely from England is actually a *Neogastroplites* and not a malformed *Callihoplites* as suggested by Spath (10, p. 224). Seely's type came from the Cambridge Greensand, a bed correlative with the "fish scale" horizon of Western Canada at the contact of the Upper and Lower Cretaceous. These are the beds where the *Gastroplites* stocks showed maximum evolutionary explosion as exemplified by *Neogastroplites* itself.

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