ALBIAN AMMONITE FAUNAS FROM PERU: THE GENUS NEODESHAYESITES

CASEY, 1964

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INTRODUCTION

Our understanding of the Cretaceous ammonite succession of Peru is mainly based on the reference work of Benavides Cáceres (1956) that updates the descriptive paleontological papers by Gabb (1877), Sommermeier (1910), and Knechtel et al. (1947), among others. New fossil collections made in the course 1995 and 1999 in northern and central Peru provide the basis for a revision of the Albian ammonite faunas of this country. In contrast to our predecessors, our collections are based on sections that have been sampled bed by bed.

The present study concentrates on the Early Albian ammonites from the Inca Formation of northern Peru. These forms were previously described as Pararhoplitites nicholsoni Benavides Cáceres, 1956, P. inti Benavides Cáceres, 1956, and P. quilla Benavides Cáceres, 1956. Comparison of the Peruvian specimens with material from Colombia has convinced us that these taxa should be placed in Neodeshayesites Casey, 1964. As interpreted herein, Neodeshayesites is a representative of Acanthohoplitinae that also includes species from Texas previously assigned to Hypacanthoplites Spath, 1923 and Parahoplites Anhula, 1899 (Scott, 1940; Young, 1974). The paleogeographic distribution of the genus is restricted to the New World and includes Colombia, Venezuela, Texas, and Peru.

STRATIGRAPHIC SUMMARY AND FOSSIL LOCALITIES

The newly collected Neodeshayesites come from the Baños del Inca and Tamberia Oeste sections in the department of Cajamarca in northern Peru. The first section is situated north of Baños del Inca, 10 km east of the city of Cajamarca, in the direction of Quebrada Otuzco. The second lies northwest of Algodón, near the Hacienda Tamberia, 20 km west of Aguas Calientes and near the junction of the Cajamarca and Crisnejas Rivers (Fig. 1).

Our specimens originate from the Andean Basin, which was controlled by the development of a magmatic arc along the Peruvian margin during the Lower and Mid-Cretaceous (Mégard, 1978). They were collected from the Inca Formation, which is characterized by mixed carbonate-siliclastic marine deposits that mark the base of a major regional transgression which started in the Albian and reached its climax during the Turonian (Jaillard et al., 2000).

The Neodeshayesites marked the first faunal associations of the Early Albian and defined the umbilicostatus and nicholsoni biohorizons of the nicholsoni Zone (Robert, 2002) (Fig. 2.1). The fauna associated with Neodeshayesites at Baños del Inca includes “Beudanticeras” sp., Platiknemiceras sp., Hamites cf. pseudatenuatus Casey, 1961, Hamites sp., and Douvilleiceras rex (Scott, 1940) (Fig. 2.4). The Neodeshayesites from the Tamberia Oeste section are associated with “Beudanticeras” gr. dupiniyanum (d’Orbigny, 1841)-newtonii Casey, 1961, “Beudanticeras” chimuense (Benavides Cáceres, 1956), Glottoceras sp., Douvilleiceras aff. argentinum (White, 1887), and Douvilleiceras sp. (Fig. 2.2).

SYSTEMATIC PALEONTOLOGY

Specimens labeled ISEM are housed at the Institut des Sciences de l’Évolution de Montpellier. Material labeled as ERC is kept in the paleontological collections at the Université Paul Sabatier (Toulouse). Type and figured specimens from the American Museum of Natural History, New York (AMNH), and the Texas Memorial Museum, Austin (BEG), have also been examined for this study.

Order AMMONOIDEA Zittel, 1884

Suborder AMMONITINA Hyatt, 1889

Superfamily DESHAYESITACEAE Stoyanow, 1949

Family DESHAYESITIDAE Stoyanow, 1949

Subfamily ACANTHOHOPLITINAE Stoyanow, 1949

Discussion.—Stoyanov (1949, p. 95) created the subfamily Acanthohoplitinae for tuberculate forms with radial or falcate ribs and sutures with asymmetrical first lateral lobes which cross the umbilical border on the level of the second lateral saddle. The original scope of the subfamily included the genera Acanthohoplitites Sinzov, 1907, Immunitoceras Stoyanow, 1949, Paracanthohoplitites Stoyanow, 1949, Hypacanthoplites, and Colombliticeras Spath, 1923. Later, Casey (1954) added the genus Gargasiceras Casey, 1954.

Casey (1964) originally placed the genus Neodeshayesites in the subfamily Deshayesitinae. He nevertheless noted that the ornament shows clear affinities with the Acanthohoplitinae. The Peruvian specimens confirm Casey’s (1964) observations. As interpreted herein, Neodeshayesites includes a group of ammonites characterized by Deshayesites- to Dufrenoya-like early ornament, followed quickly by the development of straight and well-elevated ribs similar to those of Hypacanthoplites. We follow Casey (1964) in considering that this type of ribbing, combined with a tendency to modify the curve of the lateral ribs from sigmoidal to biconvex, indicates a closer relationship with the Acanthohoplitinae than with any known Deshayesitinae. Moreover, the typically arched venter that characterizes the adult stage of all species of Neodeshayesites is a very distinctive feature that is unknown in any other genus of the subfamily Acanthohoplitinae (e.g., Hypacanthoplites, Acanthohoplitites, etc.) (Robert, 2002). On the basis of these new observations, we assign the genus Neodeshayesites to the subfamily Acanthohoplitinae.

The Acanthohoplitinae is restricted to the late Early Aptian to Early Albian (Casey, 1965; Wright et al., 1996; Bogdanova and Prozorovsky, 1999).

Genus NEODESHAYESITES Casey, 1964

Type species.—Deshayesites stutzeri Riedel, 1937; by original designation of Casey (1964, p. 289, footnote). The lectotype of D. stutzeri is the specimen figured by Riedel (1937, pl. 7, figs. 5, 6) by the subsequent designation of Robert (2002).

Discussion.—In addition to the species originally included in Neodeshayesites by Casey (1964), we agree with Etyao Serna (1979) that Ammonites karsteni Rocas, 1875, Neodeshayesites albertoalvarezi Etyao Serna, 1979, and N. cingulatum Etyao Serna, 1979, belong in the genus.

Our recent investigations in the Early Albian of Peru and the revision of faunas of similar age from Texas have convinced us
ornament limited to primary and secondary ribs with rarely more
develop a rounded venter and convex flanks and both develop
of Early Albian Acanthohoplitinae in the New World: (Robert, 2002), shows the existence of two morphological groups
and Arizona described by Scott (1940), Stoyanow (1949), and
ical differences are reduced and the distinction between
and

that several species previously referred by Scott (1940), Benavides Cáceres (1956), and Young (1974) to Parahoplites and Hypacanthoplites belong in Neodeshayesites. These are Parahoplites nicholsoni, P. quilla, P. intii, Parahoplites umbilicostatus Scott, 1940, Hypacanthoplites mayfieldensis Scott, 1940, and Hypacanthoplites comalensis Young, 1974 non Scott, 1940.

Examination of representatives of Neodeshayesites from Texas and Arizona described by Scott (1940), Stoyanow (1949), and Young (1974), coupled with the study of Peruvian specimens (Robert, 2002), shows the existence of two morphological groups of Early Albian Acanthohoplitinae in the New World:

1. A “Hypacanthoplites” morphological pole, with hexagonal to rectangular whorl sections and flattened venters, and sub-
radial or falcate ribs which bifurcate from lateral tubercles, are bent on the ventral shoulder, and tuberculate on the um-
bilical border. The lateral tubercles are situated under the in-
volution line (see the type species Hypacanthoplites milleti-
anus d’Orbigny, 1841, pl. 77, figs. 1, 2, 4, 5) and

2. A “Neodeshayesites” morphological pole, with subquadrate
to oval whorl sections and flattened venters on the younger
stages that become rounded on the body chamber. The ribs are simple and bend gently forward on the lower half of the
flank, giving a typically sinuous aspect to the ornament. Pri-
mary and secondary ribs alternate irregularly and project straight across the venter. Tubercles are generally absent, al-
though the inner whorls of N. nicholsoni (Benavides Cáceres, 1956) bear small lateral tubercles (see the type species Neo-
deshayesites stutzeri Riedel, 1937, pl. 7, figs. 5, 6).

On the late adult stages of large macroconchs, the morpholog-
cal differences are reduced and the distinction between Hypa-
canthoplites and Neodeshayesites becomes critical. Both groups
develop a rounded venter and convex flanks and both develop
ornament limited to primary and secondary ribs with rarely more
than two successive short ribs. The distinction between these gen-
era is therefore largely based on differences in the early and mid-
dle ontogenetic stages.

Neodeshayesites shows strong affinities with the genus Immu-
nitoceras, which was considered a synonym of Hypacanthoplites
by Young (1974). Both of these genera share common morpho-
logical characters which developed identically during ontogeny.
These include single primary ribs which bifurcate or alternate
irregularly with secondaries. The ribs are elevated on the peri-
umbilical area, falcate on the flanks, and cross the venter without
interruption. The venters of both genera change from tabulate to
rounded during ontogeny and the whorl sections are subquadrate
in the juvenile whors and oval in the adult stages. However, in
opposition of Young (1974), the genus Neodeshayesites is herein
distinguished from Immunitoceras by its smaller umbilicus and
the earlier appearance of a rounded form of the venter. These
morphological similarities and their respective stratigraphic rang-
es—late Late Aptian to ?earliest Early Albian for Immunitoceras
and Early Albian for Neodeshayesites—suggest an ancestor/de-
scent relationship between the two genera.

Renz (1982) placed the genus Neodeshayesites in synonymy
with Deshayesites Kasansky, 1914. He suggested that the mor-
phologic particularities of the Venezuelan population, mentioned
by Casey (1964), have to be linked with “special environmental
conditions [of the La Luna Formation] and should not influence
taxonomy above the species level.” In addition to the long time
span that separates the last Deshayesites of the grandi group
(Early Aptian) and the first Neodeshayesites (Early Albian), it
should be emphasized that Neodeshayesites has been recovered
from a wide range of environmental contexts. The Inca Formation
of Peru and the El Ocal Formation of Colombia (Etayo Serna and
Carrillo Castillo, 1996) comprise shallow water shelf deposits
characterized by mixed carbonate-siliclastic sediments. However,
Neodeshayesites also occurs in Colombia and Texas in deeper
water deposits characterized by the dark shales, calcareous con-
cretions, and limestones of the Capotes Member (Etayo Serna,
1979) and the nodular marly limestones and blue marls of the
Cuchillo Formation (Sellards et al., 1954). Therefore, Renz’s ar-
gument for an environmental intrageneric adaptation cannot be
retained. As a whole, and in contrast to many other ammonite
groups (see Kennedy and Cobban, 1976), the distribution of gen-
era in the subfamily Acanthohoplitinae does not seem to “facies-
linked.” This may explain their highly successful dispersal and
cosmopolitan distribution.

Neodeshayesites umbilicostatus (Scott, 1940)

Figure 3.1–3.7

Parahoplites umbilicostatus Scott, 1940, p. 1029–1030, pl. 62, fig. 8; pl. 63, fig. 10.
Hypacanthoplites umbilicostatus (Scott). Young, 1974, pl. 13, figs. 1, 6.
non Hypacanthoplites umbilicostatus (Scott). Young, 1974, pl. 16, fig. 8 (=Neodeshayesites mayfieldensis Scott, 1940).

Description.—Our material adds nothing to the knowledge of
the early stages of the species. For example, ISEM-99-110Eb-01
(Fig. 3.1, 3.2) is tentatively considered to represent the adult stage
of Neodeshayesites umbilicostatus, which suggests that adult size
may have reached a diameter of at least 170 mm (Table 1). At
this stage, ribbing tends to lose its sinuoidal aspect. ERC-99-
110Eb-02 (Fig. 3.3) is a fragmentary phragmocone almost iden-
tical to the holotype. This similarity is enhanced by the crushed
preservation. ISEM-99-110Eb-05 (Fig. 3.4) is a large imprint that
shows perfectly the sculpture at a diameter similar to that of the
holotype, leaving no doubt as to its conspecificity. A portion of
the internal mold of the same specimen shows the shape of the

Figure 1.—Map of the Albian Occidental Peruvian Basin showing the
Baños del Inca and Tamberia Oeste localities, and their geographic and
topographic positions, respectively. Details extracted from the 1/250,000 Topographic Map of Cajamarca (SB 17–16) of the National
Geographic Institut (IGN) of Peru.

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Figure 2—Stratigraphic framework of the Early Albian of central and northern Peru. 1, Biostratigraphic nomenclature. Late Early Albian biozones, subzones, and biohorizons defined by *Neodeshayesites* Casey, 1964 index species, characterization of the subdivision limits, formations, and type sections. 2, Section at Baños del Inca. Lithologic log, faunal succession (ammonites, echinoderms, and bivalves), and biostratigraphic subdivision. 3, Legend. 4, Section at Tamberia Oeste. Lithologic log, faunal succession (ammonites, echinoderms, and bivalves), and biostratigraphic subdivision.
whorl section (Fig. 3.4), which is confirmed by specimen ERC-95-I9-08 (Fig. 3.5–3.7).

Types.—According to Scott (1940, p. 1029), *Neodeshayesites umbilicostatus* is a fairly common ammonite in the southern Quitman Mountains (Texas, USA), but the preservation of the material is so bad that the species is mainly based on the holotype (BEG 34817). This specimen is too crushed and fragmentary to be measured precisely, nevertheless its diameter should not have exceeded 90 mm. Recent examination of the specimen has shown that the inner whorls have been damaged since the original description was assured precisely, nevertheless its diameter should not have exceeded 34817. This specimen is too crushed and fragmentary to be measured.

<table>
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<th>D</th>
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<th>Wh</th>
<th>Wb/Wh</th>
<th>Ud</th>
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<td><strong>Dimensions (mm) of <em>Neodeshayesites inti</em> (Benavides Cáceres, 1956)</strong></td>
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<td><strong>Dimensions (mm) of <em>Neodeshayesites sp. juv.</em></strong></td>
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<td>11.5</td>
<td>14.5</td>
<td>0.79</td>
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D = diameter; Wb = whorl breadth; Wh = whorl height; Ud = umbilical diameter.

Figures in parentheses are dimensions as a percentage of diameter.

****Material examined.****—Seven more or less fragmentary specimens (ERC-95-I9-06, ERC-95-I9-08, ISEM-99-I10Eb-01, ERC-99-I10Eb-02, ISEM-99-I10Eb-03, ISEM-99-I10Eb-05, ISEM-99-I9C-06). Occurrence.—The holotype is from the “Blue marls” of the Cuchillo Formation (locality M1, see text-fig. 15 in Young, 1974, p. 207), in the southern Quitman Mountains, Hudspeth County, West Texas. According to Young (1974), the biostratigraphic position of this species is unclear because the associated fauna listed by Scott (1940) includes species from more than one ammonite zone. Our material was collected from the lowest part of the Inca Formation. Five specimens were found loose at...
bed 7 and 9 (samples I10Eb), while the others were collected in situ from beds 17 to 24 (samples I9) in the Baños del Inca section (Fig. 2.4). The associated fauna (see stratigraphic summary) indicates the Early Albian umbilicostatus biohorizon (Nicholsoni Zone; Fig. 2.1) that most probably correlates in part with the Chalensis Zone of the European standard ammonite scale (see discussion in Robert et al., 1998; Robert, 2002).

Discussion.—The specimen figured by Young (1974, pl. 16, fig. 8) as Hypacanthoplites umbilicostatus shows a rectiradiate ribbing pattern that is closer to Neodeshayesites mayfieldensis than to N. umbilicostatus.

Stoyanoviceras treffryanus (Karsten, 1858) figured by Etayo Serna (1979, pl. 5, fig. 3), and considered a synonym of Immunitoceras immunitum Stoyanov, 1949 by Robert (2002), shows costulation that is very similar (particularly the falcate ribs) to nitoceras immunitum Stoyanov, 1949 by Roberts (2002), shows costulation that is very similar (particularly the falcate ribs) to nitoceras immunitum Stoyanov, 1949 by Roberts (2002).

\[ \text{Immunitoceras immunitum} \]

German specimens of Hypacanthoplites elegans (Fritel, 1906) figured by Kennedy et al. (2000, pl. 38, fig. a–k; pl. 55, fig. j, k) also present falcate ribs similar to Neodeshayesites umbilicostatus. The large specimen from Vöhrum (Kennedy et al., 2000, pl. 55, fig. j–k) possesses a large whorl section with a vertical umbilical wall that is virtually identical to that of N. umbilicostatus. Nevertheless, the German H. elegans is distinguished from N. umbilicostatus by its flat venter and the retention of falcate ribbing into the adult stage. It reaches dimensions very rare in European populations but often observed in Peruvian taxa. Its large size is a single case and so is not characteristic. It does not permit us to assume synonymy with N. umbilicostatus.

Neodeshayesites inti (Benavides Cáceres, 1956) Figure 3.8–3.12

Hypacanthoplites mayfieldensis Scott, 1940, pl. 63, figs. 3–6.

Parahoplites inti Benavides Cáceres, 1956, p. 441–442, pl. 42, figs. 9, 10.

Hypacanthoplites mayfieldensis (Scott). Young, 1974, pl. 14, figs. 1, 2, 6, text-figs. 6c, 7d.

Hypacanthoplites umbilicostatus (Scott). Young, 1974, pl. 16, fig. 8.

Description.—The largest example in our collection (Fig. 3.9, 3.10) is fully septate at an estimated diameter of 123 mm (Table 1) and shows an ovigal whorl section, higher than wide. Primary and secondary ribs are almost straight and intercalatories are faint and rare, ISM-95-19B-08 is the best-preserved representative of the species. It shows a small portion of the inner whorls (Fig. 3.8) that indicates that prorsiradiate ribs branch just above the umbilical wall at younger growth stages. Middle growth stages, similar to the holotype, are well expressed by MPUP-95-19-04, which shows ontogenetic modification toward the advanced stages described above. At its smaller diameter, the section of this specimen is oviparous (Fig. 3.11, 3.12) and very similar to figure 26 of Benavides Cáceres (1956, p. 441).

Types.—Neodeshayesites inti was originally described on the basis of two specimens. The holotype (AMNH 27390/1) has been described in great detail by Benavides Cáceres (1956, p. 440). There is little to add to the original diagnosis, except that the specimen corresponds to a mature microconch.

Other material examined.—Fourteen type specimens representing all growth stages. Most of the specimens are fragmentary, but ontogeny, intraspecific variation, and probable dimorphism are well illustrated by the specimens in Figures 3.13–3.21.

Occurrence.—The holotype is from bed 6 of the Inca Formation at Tarabiera. Additional material has been recorded from Sunchubamba (Benavides Cáceres, 1956). Our material is from the middle part of the Inca Formation in the Tarabiera Oeste section (bed 17). All but five specimens were collected in situ (Fig. 2.2). The associated fauna (see stratigraphic summary) indicates the nicholsoni biozone of the Early Albian nicholsoni Biozone (Fig. 2.1).

Discussion.—Representatives of Hypacanthoplites comalensis figured by Young, (1974, pl. 16, fig. 1, text-fig. 6i) are morphologically similar to Neodeshayesites nicholsoni: a tabulate venter in younger stages that became rounded in adult stages; a wide umbilicus and high periumbilical wall; rectiradiate and strong primary ribs which develop elongated bullae on the lower third of the flank; and frequent intercalatory ribs on the upper half of the flank.

Renz (1982, pl. 1, fig. 3a, b) figured a specimen, identified as Deshayesites? nodosus, characterized by Dufrenoya-like early ornament with a tabulate venter and distinct, elongated periumbilical tubercles. It is herein assigned to Neodeshayesites nicholsoni.

The inner whorls of Neodeshayesites nicholsoni show similarities to Immunitoceras immunitum: a moderately evolve umbilicus; the presence of periumbilical tubercles; and primary ribs spaced and separated by thin secondary ribs. Nevertheless, the reduction of the ribs on the flank and the high dimension of the tubercles is typical of N. nicholsoni.
Early Albian associations of Peru, Colombia, and Venezuela, but Acanthohoplitinae of the New World. It dominates the middle Neodeshayesites Biozone (Fig. 2.1).

Material examined.—Five specimens (MPUP-95I9.09, MPUP-95I9.10, MPUP-95I9B.06, MPUP-99I9B.04, ERC-99I9C.04) and the holotype of Parahoplites quilla (AMNH 27391/1).

Occurrence.—The present specimens were collected in situ from the basal part of the Inca Formation at the Bahos del Inca section (samples 19; Fig. 2.4). As previously noted, this level represents the Early Albian umbilicostatus horizon of the nicholsoni Biozone (Fig. 2.1).

Discussion.—The specimens included in this section could represent the juvenile stages of either Neodeshayesites inti or N. umbilicostatus. At diameters less than 20 mm, ERC-99-19C-04 (Fig. 3.22, 3.23) shows two rows of tiny tubercles on the ventrolateral shoulders that recall Hypacanthoplites. This feature is also expressed on the type material of Neodeshayesites stutzeri figured by Riedel (1937).

Since the type material of Parahoplites quilla is based on fragments of juvenile specimens that strongly resemble our material (Fig. 3.22–3.25) from an equivalent level at the same locality, we suggest that this species be regarded as a nomen dubium.

Conclusions
Analysis of new collections of Peruvian Acanthohoplitinae and revision of the type specimens described by Benavides Cáceres (1956) from Peru, and by Scott (1940) and Young (1974) from Texas (USA), suggests a new interpretation of the Acanthohoplitinae:

1. the genus Neodeshayesites is transferred from the Deshayesitinae to the Acanthohoplitinae;
2. two morphological groups are distinguished in the Early Albian Acanthohoplitinae of the New World: Neodeshayesites, which is widespread from the Andes to the southwestern USA, and Hypacanthoplites, which does not seem to occur outside Texas and adjacent Mexico; and
3. the species quilla, inti, nicholsoni, and umbilicostatus, previously assigned to Parahoplites and Hypacanthoplites, are transferred to the genus Neodeshayesites.

These interpretations, coupled with a new stratigraphic approach, allow us to reconsider the content and paleobiogeographic significance of the genus Neodeshayesites. Parahoplites quilla corresponds to a juvenile Neodeshayesites and is herein regarded as a nomen dubium. Neodeshayesites represents the youngest Acanthohoplitinae of the New World. It dominates the middle Early Albian associations of Peru, Colombia, and Venezuela, but it is also present in the Early Albian of Texas.

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