J. Paleont., 79(3), 2005, pp. 611–618

0022-3360/05/0079-611$03.00

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 *Parahoplites 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* Anthula, 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. *pseudattenuatus* Casey, 1961, *Hamites* sp., and *Douvilleiceras rex* (Scott, 1940) (Fig. 2.4). The *Neodeshayesites* from the Tamberia Oeste section are associated with "*Beudanticeras*" gr. *dupinianum* (d'Orbigny, 1841)-*newtoni* Casey, 1961, "*Beudanticeras*" *chimuense* (Benavides Cáceres, 1956), *Glottoceras* sp., *Douvilleiceras offarcinatum* (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 DESHAYESITOIDEA 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 *Acanthohoplites* Sinzov, 1907, *Immunitoceras* Stoyanov, 1949, *Paracanthoplites* Stoyanov, 1949, *Hypacanthoplites*, and *Colombiceras* 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 biconcave, 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*, *Acanthohoplites*, 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 Etayo Serna (1979) that *Ammonites karsteni* Marcou, 1875, *Neodeshayesites albertoalvarezi* Etayo Serna, 1979, and *N. cingulatum* Etayo 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

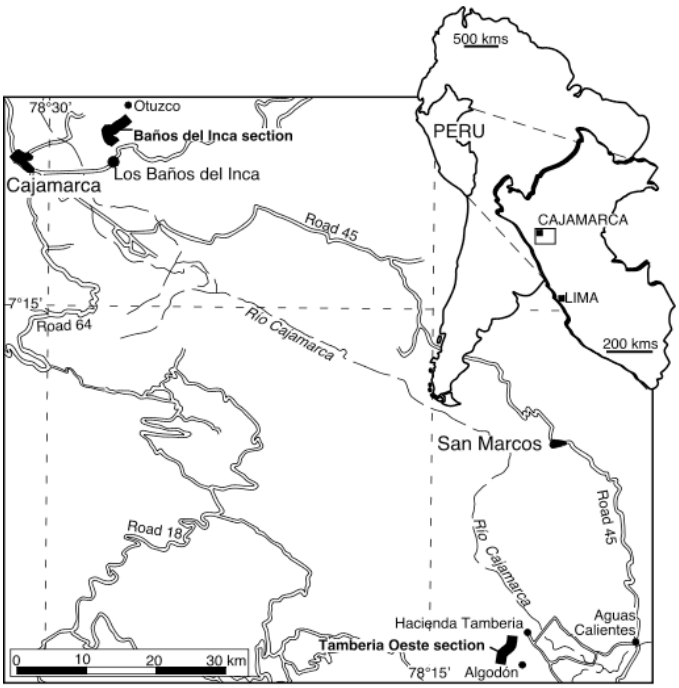

FIGURE *1*—Map of the Albian Occidental Peruvian Basin showing the Baños del Inca and Tamberia Oeste localities, and their geographic and topographic positions, respectively. Details extracted from the 1/250,000 Topographic Map of Cajamarca (SB 17–16) of the National Geographic Institut (IGN) of Peru.

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. inti*, *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 subradial or falcate ribs which bifurcate from lateral tubercles, are bent on the ventral shoulder, and tuberculate on the umbilical border. The lateral tubercles are situated under the involution line (see the type species *Hypacanthoplites milletianus* 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. Primary and secondary ribs alternate irregularly and project straight across the venter. Tubercles are generally absent, although the inner whorls of *N. nicholsoni* (Benavides Cáceres, 1956) bear small lateral tubercles (see the type species *Neodeshayesites stutzeri* Riedel, 1937, pl. 7, figs. 5, 6).

On the late adult stages of large macroconchs, the morphological differences are reduced and the distinction between *Hypacanthoplites* 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 genera is therefore largely based on differences in the early and middle ontogenetic stages.

Neodeshayesites shows strong affinities with the genus *Immunitoceras*, which was considered a synonym of *Hypacanthoplites* by Young (1974). Both of these genera share common morphological characters which developed identically during ontogeny. These include single primary ribs which bifurcate or alternate irregularly with secondaries. The ribs are elevated on the periumbilical 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 whorls 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 ranges—late Late Aptian to ?earliest Early Albian for *Immunitoceras* and Early Albian for *Neodeshayesites*—suggest an ancestor/descendant relationship between the two genera.

Renz (1982) placed the genus *Neodeshayesites* in synonymy with *Deshayesites* Kasansky, 1914. He suggested that the morphologic 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 *grandis* 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 concretions, 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 argument 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 genera 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-I10Eb-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 sinusoidal aspect. ERC-99-I10Eb-02 (Fig. 3.3) is a fragmentary phragmocone almost identical to the holotype. This similarity is enhanced by the crushed preservation. ISEM-99-I10Eb-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

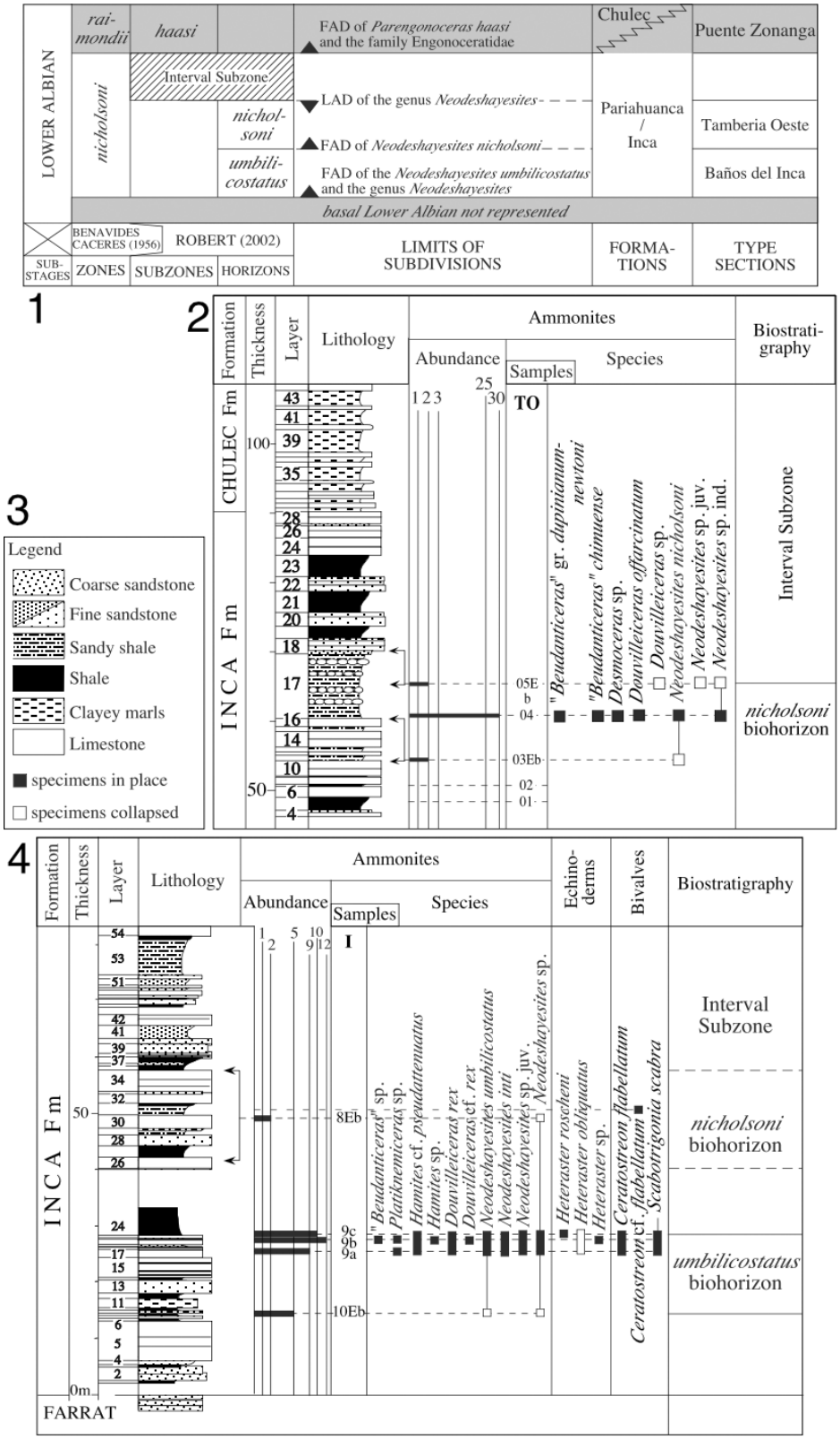

FIGURE 2—Stratigraphic framework of the Early Albian of central and northern Peru. *1,* Biostratigraphic nomenclature. Late Early Albian biozones, subzones, and biohorizons defined by *Neodeshayesites* Casey, 1964 index species, characterization of the subdivision limits, formations, and type sections. *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.

TABLE 1—Measurements of specimens of *Neodeshayesites umbilicostatus* (Scott, 1940), *Neodeshayesites inti* (Benavides Cáceres, 1956), *Neodeshayesites nicholsoni* (Benavides Cáceres, 1956), and *Neodeshayesites* sp. juv.

Specimen	D	Wb	Wh	Wb/Wh	Ud
Dimensions (mm) of *Neodeshayesites umbilicostatus* (Scott, 1940)					
ERC-95-I9-06	80 (100)	20 (25)	28 (35)	0.71	— (—)
ERC-95-I9-08	— (—)	20.5 (—)	23 (—)	0.89	— (—)
ISEM-99-I10Eb-01	170 (100)	48 (28.2)	69 (40.6)	0.7	— (—)
ERC-99-I10Eb-02	95 (100)	— (—)	34.5 (36.3)	—	22 (23.2)
ISEM-99-I10Eb-03	— (—)	35 (—)	41 (—)	0.85	— (—)
ISEM-99-I10Eb-05	75 (100)	— (—)	32 (42.7)	—	22 (29.3)
ISEM-99-I9C-06	— (—)	— (—)	32 (—)	—	— (—)
Dimensions (mm) of *Neodeshayesites inti* (Benavides Cáceres, 1956)					
ISEM-95-I9-04	80 (100)	24 (30)	27 (33.7)	0.89	— (—)
ERC-95-I9B-04	105 (100)	30 (28.6)	35 (33.3)	0.86	— (—)
ISEM-95-I9B-08	95 (100)	35 (36.8)	38.5 (40.5)	0.91	22 (23.2)
ISEM-99-I9A-03	120 (100)	41 (34.2)	46 (38.3)	0.89	— (—)
Dimensions (mm) of *Neodeshayesites nicholsoni* (Benavides Cáceres, 1956)					
ISEM-99-TO3Eb-02	—	50 (—)	61 (—)	0.82	— (—)
ISEM-99-TO4-26	95 (100)	32.5 (34.2)	39 (41.1)	0.83	35 (36.8)
ISEM-99-TO4-27	97 (100)	34 (35.1)	39 (40.2)	0.87	33 (34)
ERC-99-TO4-28	80 (100)	29 (36.2)	32 (40)	0.91	— (—)
ERC-99-TO4-29	120 (100)	37.5 (31.2)	44 (36.7)	0.86	— (—)
ERC-99-TO4-30	150 (100)	39.6 (26.4)	55 (36.7)	0.72	— (—)
ISEM-99-TO4-31	65 (100)	22 (33.8)	26 (40)	0.85	— (—)
ISEM-99-TO4-32	55 (100)	20.5 (37.3)	22.3 (40.6)	0.92	— (—)
ISEM-99-TO4-33	41 (100)	14.2 (34.6)	18.5 (45.1)	0.77	9 (22)
ISEM-99-TO4-34	50 (100)	18.5 (37)	20 (40)	0.92	17 (34)
ERC-99-TO4-36	70 (100)	25.6 (36.6)	30 (42.9)	0.86	— (—)
ERC-99-TO4-38	45 (100)	17.6 (39.1)	21 (46.7)	0.84	— (—)
ERC-99-TO4-40	70 (100)	21.5 (30.7)	26 (37.1)	0.83	— (—)
ERC-99-TO4Eb-02	50 (100)	18 (36)	22 (44)	0.82	— (—)
Dimensions (mm) of *Neodeshayesites* sp. juv.					
ISEM-95-I9-09	35 (100)	— (—)	13 (37.1)	—	— (—)
ISEM-95-I9-10	37 (100)	14.5 (39.2)	17 (45.9)	0.86	— (—)
ISEM-95-I9B-06	50 (100)	18.5 (37)	— (—)	—	— (—)
ISEM-99-I9B-04	45 (100)	16 (35.6)	19.5 (43.3)	0.82	— (—)
ERC-99-I9C-04	40 (100)	11.5 (28.7)	14.5 (36.2)	0.79	— (—)

D = diameter; Wb = whorl breadth; Wh = whorl height; Ud = umbilical diameter.
Figures in parentheses are dimensions as a percentage of diameter.

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 umblicostatus* 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 by Scott (1940). This could already be noticed on Young's (1974) more recent figure of the specimen.

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

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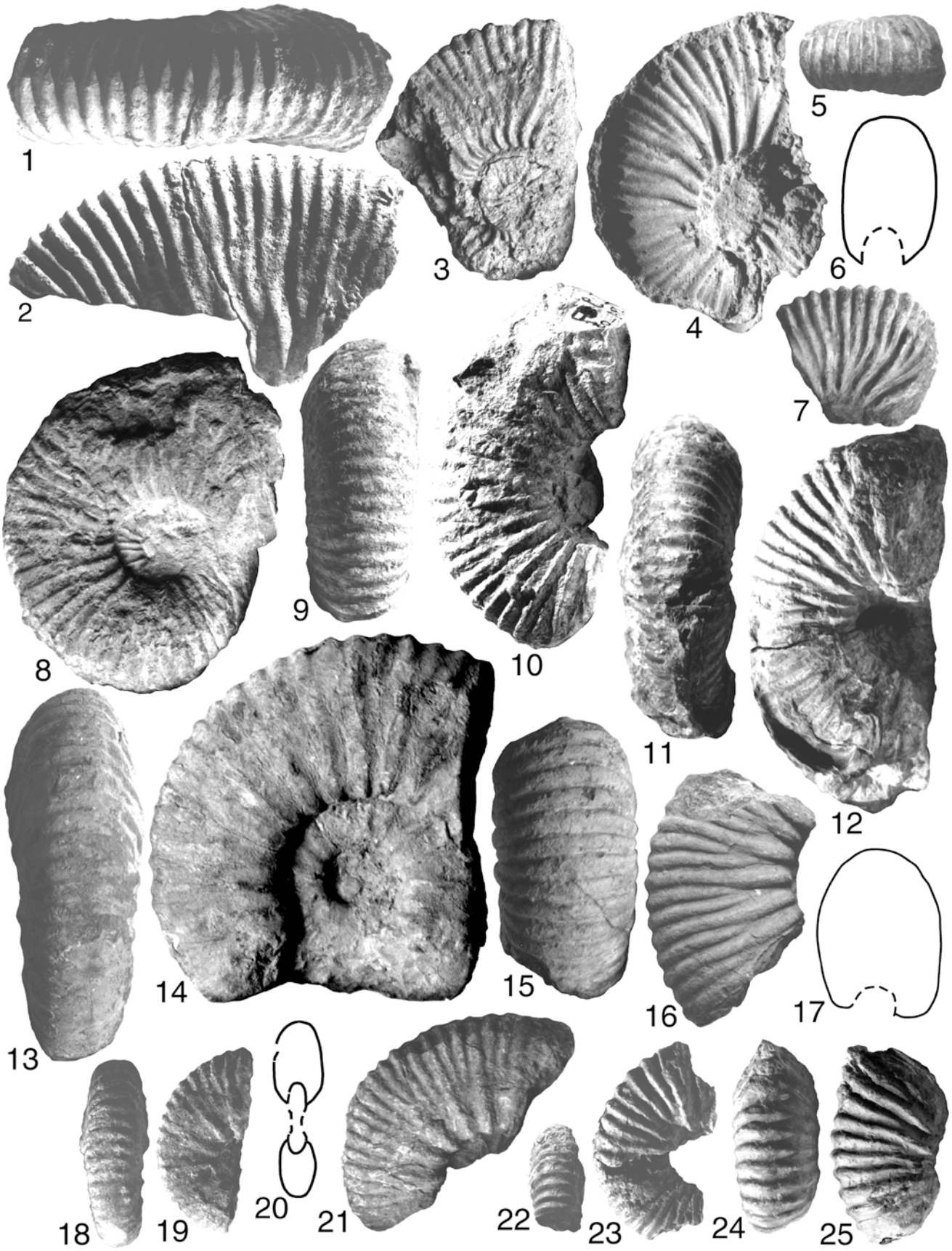
FIGURE 3—*1–7, Neodeshayesites umbilicostatus* (Scott, 1940). *1, 2,* ISEM-99-I10Eb-01, Baños del Inca section, late Early Albian, ventral and lateral views (×0.5). *3,* ERC-99-I10Eb-02, Baños del Inca section, late Early Albian, lateral view (×0.75). *4,* ISEM-99-I10Eb-05, Baños del Inca section, late Early Albian, internal mold, lateral view (×0.75). *5–7,* ERC-95-I9-08, from Baños del Inca section, late Early Albian, ventral view, section, and lateral view (×0.75). *8–12, Neodeshayesites inti* (Benavides Cáceres, 1956). *8,* ISEM-95-I9B-08, Baños del Inca section, late Early Albian, lateral view (×0.75). *9, 10,* ISEM-99-I9A-03, Baños del Inca section, late Early Albian, ventral and lateral views (×0.5). *11, 12,* ISEM-95-I9-04, Baños del Inca section, late Early Albian, ventral and lateral views (×0.75). *13–20, Neodeshayesites nicholsoni* (Benavides Cáceres, 1956). *13, 14,* ISEM-99-TO4-26, Tamberia Oeste section, late Early Albian, ventral and lateral views (×0.75). *15–17,* ERC-99-TO4-29, Tamberia Oeste section, late Early Albian, ventral and lateral views and section (×0.75). *18–20,* ISEM-99-TO4-33, Tamberia Oeste section, late Early Albian, ventral and lateral views and section (×1). *21,* ERC-99-TO4-28, Tamberia Oeste section, late Early Albian, lateral view (×1). *22–25, Neodeshayesites* sp. juv. *22, 23,* ERC-99-I9C-04, Baños del Inca section, late Early Albian, ventral and lateral views (×1). *24, 25,* ERC-99-I9B-04, Baños del Inca section, late Early Albian, ventral and lateral views (×1).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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*.

Stoyanowiceras 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 *Neodeshayesites umbilicostatus*.

German specimens of *Hypacanthoplites elegans* (Fritel, 1906) figured by Kennedy et al. (2000, pl. 38, fig. a–k; pl. 55, fig. j, k) also presents 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 ogival whorl section, higher than wide. Primary and secondary ribs are almost straight and intercalatories are faint and rare. ISEM-95-I9B-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-I9-04, which shows ontogenetic modification toward the advanced stages described above. At its smaller diameter, the section of this specimen is ovoid (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 27392) is a deformed and incomplete specimen that corresponds to the middle growth stages.

Other material examined.—Four more or less fragmentary topotypes (ISEM-95-I9-04, ERC-95-I9B-04, ISEM-95-I9B-08, ISEM-99-I9A-03).

Occurrence.—The holotype is from the basal part of the Inca Formation (bed 50 of the Baños del Inca section, Benavides Cáceres, 1956, p. 442). Our specimens were collected in situ from an equivalent level at the type locality (samples I9; Fig. 2.4). The associated fauna (see stratigraphic summary) indicates the Early Albian *umbilicostatus* biohorizon (*nicholsoni* Biozone; 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.—*Neodeshayesites inti* differs from *Neodeshayesites umbilicostatus* by its sharper ribs, stronger ornament, and ovoid whorl section. Nevertheless, the large specimen of *N. umbilicostatus* (Fig. 3.1, 3.2) suggests close affinities between the two species. Because of overlap in stratigraphic distribution, the two taxa may represent a dimorphic pair. Nevertheless, the material at our disposal is much too fragmentary to assume fully this hypothesis. *Hypacanthoplites mayfieldensis* is very similar to *Neodeshayesites inti* in ornament, size, and stratigraphic distribution. Again, the preservation of the type material from Texas does not allow us to assume synonymy between the two species.

NEODESHAYESITES NICHOLSONI (Benavides Cáceres, 1956)
Figure 3.13–3.21

Parahoplites nicholsoni BENAVIDES CÁCERES, 1956, pl. 42, figs. 11, 12.
Hypacanthoplites comalensis (SCOTT). YOUNG, 1974, pl. 16, fig. 1, text-fig. 6i.
Deshayesites? *nodosus* (RIEDEL). RENZ, 1982, pl. 1, fig. 3a, b.

Description.—During early growth stages, the suspected microconch is characterized by its open umbilicus, stout ornament, and quadrate whorl section. Middle and adult stages are marked by the progressive weakening of the periumbilical bullae and changes in the shape of the whorl section from quadrate to subquadrate to at least subogival with an arched venter (Fig. 3.14, 3.15, 3.21). The umbilicus remains moderately evolute. The macroconch is characterized by less marked bullae and subquadrate whorl sections in the early whorls (Fig. 3.18–3.20). The subogival whorl section appears at an earlier stage and is maintained until the largest diameter. Although primary ribs are very coarse in both dimorphs, they never develop into tuberculate bullae as in the microconch (Fig. 3.15–3.17).

Type.—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 topotype 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 Figure 3.13–3.21.

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

NEODESHAYESITES juvenile species
Figure 3.22–3.25

Parahoplites quilla BENAVIDES CÁCERES, 1956, pl. 42, figs. 1–8.

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 Baños del Inca section (samples I9; 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-I9C-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.

ACKNOWLEDGMENTS

This work was undertaken in the frame of the Ph.D. thesis of E. Robert. We are grateful to E. Jaillard (Grenoble, France) and the members of the IRD of Lima (Peru) for financial support of the field work. We thank N. H. Landman (American Museum of Natural History, New York) for the loan of Benavides Cáceres's type material. We are also grateful to R. W. Scott (University of Tulsa) for organizing ER's field work in Texas and for introducing us to the Albian stratigraphy of Texas. We greatly thank A. Molineux (Texas Memorial Museum, Austin, Texas) for facilitating the examination of the Texas ammonite collections. And we acknowledge K. Young (University of Texas) for access to his ammonite collections. Critical reviews by W. A. Cobban and P. Rawson substantially improved the paper. We are grateful to D. M. Work for help in improving the English.

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ACCEPTED 7 JULY 2004