Jurassic-Cretaceous Biochronology and Paleogeography of North America, edited by G.E.G. Westermann, Geological Association of Canada Special Paper 27, 1984

THE ANDEAN MID-JURASSIC NEUQUENICERAS AMMONITE ASSEMBLAGE OF CUALAC, MEXICO

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ABSTRACT

Re-examination of the classic ammonite localities near Cualac in the state of Guerrero has revealed that: 1) the majority of species described by Burckhardt (1927) under Macrocephalites [Eurycephalites s.l.], Reineckeia, Peltoceras [both? Neuqueniceras s.l.] and Perisphinctes [Choffatia s.l.] occur within a relatively small stratigraphic interval of the ca. 550 m thick Yucuñuti Formation. 2) They overlie beds with scarce Epistrenoceras dated as middle Late Bathonian and, 3) range upward into a level with a latest Bathonian - earliest Callovian fauna yielding Clydoniceras inflatum n.sp., a genus hitherto known only from the Tethyan Bathonian, Reineckeia (Rehmannia) ex. gr. rehmanni, and Eurycephalites (Lilloettia) closely allied to E. tipperi from British Columbia and to the Andean E. steinmanni which at Caracoles occurs together with the Bathonian Prohecticoceras subjacent to Neuqueniceras (Frickites). 4) The highest beds yield what are probably Reineckeia s.s., Hecticoceras (H.) ex gr. hecticum indicating latest Early Callovian, and late Eurycephalites. We suggest that the Neuqueniceras assemblage is of latest Bathonian to earliest Callovian age, that the eastern Pacific E. (Lilloettia) species may be long-ranging, and that Reineckeia s.l. may have appeared earlier here than in Tethys and derived from Neuqueniceras. This assemblage occurs again with largely identical species in the Chile-Argentine Andes.

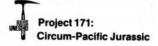
RÉSUMÉ

Un second examen des localités classiques d'ammonites près de Cualac dans l'état de Guerrero a révélé que: 1: la majorité des espèces décrites par Buckhardt (1927) comme Macrocephalites (Eurycephalites s.l.), Reineckeia, Peltoceras (à la fois (?) Neuqueniceras s.l.) et Perisphinctes (Choffatia s.l.) sont présentes

dans l'intervalle statigraphique relativement petit de la formation de Yucunuti, d'une épaisseur d'environ 550 m; 2) Elles reposent sur des couches litées contenant peu de Epistrenoceras datant de la fin du Bathonien moyen et 3) Elles évoluent vers le sommet de la formation en un niveau contenant une faune de la fin du Bathonien - début Callovien, produisant: Clydoniceras inflatum n. sp., un genre qui n'est connu, jusqu'à maintenant, que dans le Bathonien Tethyen; Reineckeia (Rehmannia) ex. gr. rehmanni; et Eurycephalites (Lilloettia) apparentées à E. tipperi, de la Colombie-Britanique, de même qu'à E. steinmanni Andéenne laquelle, à Caracoles, est associée à Prohecticoceras sousjacente à Nuequeniceras (Frickites); 4) Les couches litées supérieures produisent probablement: Reineckeia s.s., Hecticoceras (H.) ex. gr. hecticum indiquant la fin du Callovien inférieur, et Eurycephalites. Nous suggérons que l'assemblage Neuqueniceras est principalement, sinon entièrement, de la fin du Bathonien; que les espèces du Pacifique oriental E. (Lilloettia) semblent être à grande portée; et que Reineckeia s.l. peuvent être apparues, ici, avant Tethys et qu'elles proviennent de Neuqueniceras. Cet assemblage se répète, avec des espèces largement identiques, dans les Andes Argentino-Chilienne.

INTRODUCTION

The present study concerns the biostratigraphic revision of the classic Jurassic ammonoid outcrops near Cualac in the northeastern part of the state of Guerrero (Fig. 1) made known by Burckhardt (1927) and Erben (1956). From an approximately 550 m thick shaley series (Yucuñuti Formation of Erben, 1956), a number of new species described and assigned to the genera *Macrocephalites, Reineckeia* and *Peltoceras* by Burckhardt (1927) are now considered to belong to genera and sub-



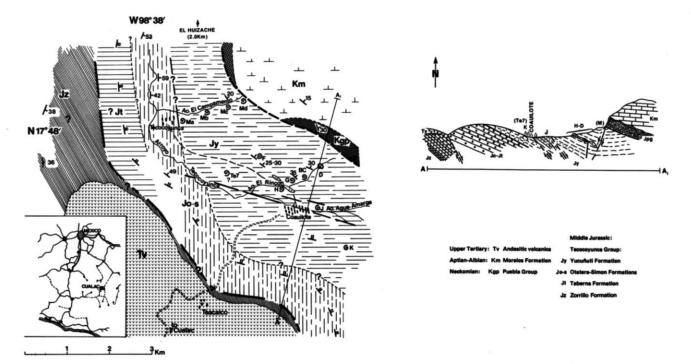


Figure 1. Geological sketch map and section of the Coauilote – Tecocoyunca area, NE Guerrero (modified from Guzman, 1950 and Erben, 1956). Our ammonoid localities marked by spirals and letters, Erben's locality by Te 7.

genera endemic to the eastern Pacific (Thierry, 1978; Cariou, 1980; Westermann, 1981; Taylor et al., this volume). A current revision of the Andean late Middle Jurassic ammonite faunas (Riccardi and Westermann, in progress), shows that the Late Bathonian-earliest Callovian faunas known mainly from west-central Argentina and northern Chile appear to be largely conspecific with the Cualac faunas. The age of these Andean faunas in terms of the (European) standard stages and zones, however, is difficult to ascertain since this time was marked by maximal biogeographic differentiation of the eastern Pacific region, the East-Pacific Realm of Westermann (1981). The classical sections of Argentina (Gottsche, 1878; Tornquist, 1898; Stehn, 1923) and Chile (Steinmann, 1881; but see Hillebrandt, 1970) have so far yielded no reliable (Tethyan) guide fossils useful for inter-realm correlation.

The Yucuñuti Formation at Coauilote (Cuahulote, etc.) near Cualac has yielded the Tethyan guide ammonite Epistrenoceras ["Cosmoceras paracontrarium" Burckhardt] elsewhere characteristic of Late Bathonian. Its stratigraphic position relative to the (East) Pacific "macrocephalitids" [recte Eurycephalitinae] and the Andean early reineckeiids [Neuqueniceras], however, has remained uncertain. Even Erben (1956), who revised the Jurassic of Guerrero and Oaxaca giving the most up-to-date Jurassic litho- and biostratigraphy of the region, made little attempt to determine the vertical ranges of the ammonites within the Yucuñuti Formation which is some 550 m thick. Furthermore, his ammonite collections were neither individually labelled nor catalogued and have never been thoroughly examined taxonomically. Only parts of his large collections housed in the Instituto de Geologia carry satisfactory stratigraphic information but the specimens are not catalogued individually. A re-examination of the classic sections as well as collecting new samples were, therefore, highly desirable.

This paper reports the results of brief field trips by the authors in 1981-82. Fuller stratigraphic and taxonomic revisions are in progress.

The area of the sections can be reached by car in dry weather only, either from Chilpacingo on Highway No. 95 (Mexico-Acapulco) via Chilapa and continuing by dirt road over mountainous terrain past Olinalá and Chaucingo, or on similar roads from Matamoros and Huamuxtitlán. The outcrop area at Coauilote-Tecocoyunca is 7 km by dirt road from Cualac. The dirt roads are in shale, ungraded, and partly with gradients steep enough to make their use hazardous or impossible in wet weather (Fig. 1). Cualac can also be reached by a small plane of the regional aviation service from Tlapa, Huamuxtitlán, Chilpancingo, Izúcar de Matamoros and Cuautla.

GEOLOGY

The rocks and geologic structure of the area of Cualac were studied by Jenny (1933), Salas (1949), Guzman (1950) and Benavides (1978), while Burckhardt (1927, 1930), Erben (1956), Alencaster (1963) and Ochoterena (1966) examined the Jurassic molluscs.

The oldest rocks are schists of the Acatlan Complex which outcrop south and west of Cualac and are dated as early Paleozoic (Ortega, 1978). Corona has recently found Permian ammonoids (dated by Westermann and confirmed by Boardman, unpublished) in the superjacent sequence of limestones and detrital sediments which were formerly placed in the Jurassic. These are followed in sequence by the Cualac Conglomerate

and the Tecocoyunca Group of the Middle (-Upper) Jurassic, Neocomian limestones, sandstones and conglomerates of the Puebla Group, and unconformably by the Middle Cretaceous limestones of the Morelos Formation. On top lie early to middle Tertiary conglomerates of the Balsas Group and andesitic rocks. Quarternary alluvia fill streams and river valleys.

The object of this paper is the Tecocoyunca Group - a clastic sequence approximately 750 m thick, of marine and continental origin. It is divided into five formations (Erben, 1956), all with conformable and transitional boundaries. From top to bottom these formations are as follows.

Yucuñuti Formation. Ca. 550 m of calcarous shales with calcareous concretions and some interbedded sandstones, particularly near the base; rich invertebrate fauna at several levels. Late Bathonian-Early (?Middle) Callovian.

Otatera Formation. 50 to 70 m of sandstones with crossstratification and shales with ferruginous concretions; some beds with oysters.

Simon Formation. 80 to 100 m of sandstones, conglomerates and beds of coal; plant remains.

Taberna Formation. 50 to 60 m of shales and siltstones with ferruginous concretions; moderately rich marine invertebrate fauna. Late Bajocian.

Zorrillo Formation. 20 to 80 m of ferruginous sandstone and shales with some coal and plant remains.

The region lies in the Sierra Madre del Sur (Morelos-Guerrero Basin). The Middle Jurassic between Coauilote and Tecocoyunca, east of Cualac (Fig. 1) belongs to the western limb of a large synclinorium. Photogeology and field work (Corona and Carrasco) indicate the presence of major faults, some of which seem to be strike-slip faults. One major fault or fault-zone runs east-south-east through the village of Coauilote. East of the village, the southern fault block dips locally 60 to 70° NE, while bedding is almost horizontal on the northern side of the fault. Other major faults are believed to be present west of Tecocoyunca, curving around the Tertiary volcanics to the south, and at the base of the Cretaceous escarpment. Small lenticular bodies of andesite form sills and probably dykes (and ? flows) in the basal sandstones of the Tecocoyunca Group and in the Yucuñuti Formation (Campa, pers. commun.).

The rate of sedimentation for the Yucuñuti Formation was high, i.e., ca. 550 m during 3 to 4 ammonoid standard zones or 20 cm. Ka-1. The basin may have subsided even more rapidly. The basal nonmarine-marine transition was followed by sandstones and shales with rich benthic brachiopod-bivalve fauna. These were superposed by the thick shales yielding almost only the pelagic ammonites described herein as well the abundant phylloceratid Ptychophylloceras and Rhaxella-like sponge spicules (Beds B-C of El Rincon section) which E. Pessagno (pers. commun.) believed to be typically abyssal. Shallowing was indicated at the top of the formation.

The principal measured section (Fig. 2) is on the ridge and along the creek bed of Arroyo El Rincon just north of Coauilote and probably equals Erben's section (1956, lam. 6, Fig. 2). The reference level is the andesite sill or flow 3 to 4 m thick at the disused road from Coauilote to Tecocoyunca (shown by Erben as sandstone with solid rectangle indicating house). The 250 m of shales with siltstones, concretions, and some lenticular sandstone beds above the reference level bear abundant ammonites between about 30 to 65 m and scarcer ammonite fauna still higher. A similar rock sequence, very approximately 200 m thick, is exposed in the lower El Rincon and upper Tecocoyunca creeks below the reference level, but it in part is repeated and possibly separated by a minor fault. Most of this lower section yielded no ammonites during our visit, but an abundant brachiopod and bivalve fauna occurred in the lower part (Alencaster, 1963). At approximately 100 to 150 m below reference is Erben's locality Te 7 from which he recorded Epistrenoceras material that cannot be found now.

East of the village of Coauilote, along the banks and near the head of Agua Amarga creek (localities J,K), we obtained several Epistrenoceras from steeply dipping, yellowish siltstone and marl beds probably indicating a fault zone (Fig. 1). The rich shallow-infaunal bivalve fauna included Vaugonia kobayashii Alencaster, Anisocardia coxi Alencaster and Unicardium cf. varicosum (Sowerby) (Alencaster, 1963). The specimens we obtained from the local villagers were said also to come from this small area.

Another important section, comprising a 350 to 400 m thick sequence which matches most of the measured section above road at El Rincon, is east of the village of Tecocoyunca along El Campamento Creek. The highest 50 to 100 m at El Campamento containing shell and sandstone beds, together with the upper limit of the formation (? faulted) are not exposed in El Rincon Creek. They comprise the youngest fossil-bearing Jurassic (Callovian) horizons known from the Coauilote-Tecocoyunca area. The top of the El Campamento section therefore, has, been projected above the El Rincon section (Fig. 2).

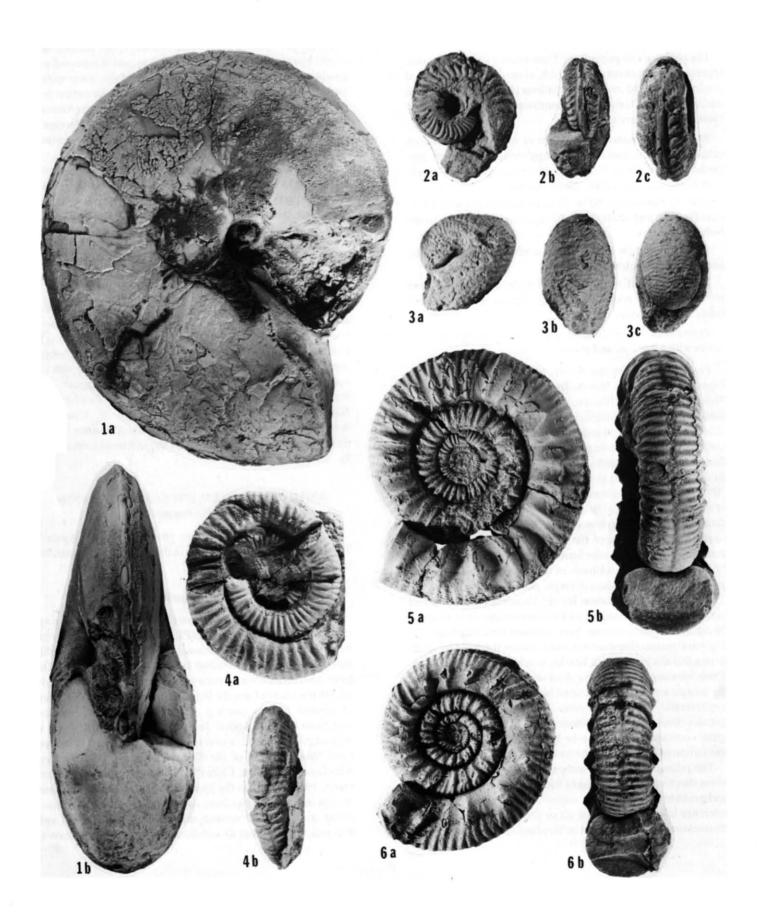
AMMONITE SYSTEMATICS (WESTERMANN) Family Phylloceratidae

Ptychophylloceras plasticum (Burckhardt), a typically Tethyan genus, is quite abundant in the middle, richly ammonitiferous part of the section.

Family Oppeliidae

Oxycerites and Paroecotraustes. Ox. (Paroxycerites) n.sp. ex gr. subdiscus (d'Orbigny) Q (Pl. I, Figs. 1a, b) and Paroecotraustes (?) cf. davaicensis (Lissajous) &, a possible dimorphic pair, have not been described from Mexico previously. The large macroconch with a tricarinate venter and rounded body chamber is known from the Upper Bathonian-Lower Callovian of western Europe (see e.g., Cariou, 1980, p. 16) and the Argentine-Chilean Andes. In fact, the rare Cualac form is indistinguishable from a new species currently being described from "beds 3 to 5" of the Cemetery section at Caracoles, Antofagasta province, Chile ("Trimarginites" part. in Westermann, 1967) and from the upper part of the Chacay Melehue section in Neuquén province, Argentina, where it is also associated with a similar smooth microconch (Westermann and Riccardi, unpublished). O. subdiscus and O. oxynotus (Leanza)

PLATE I



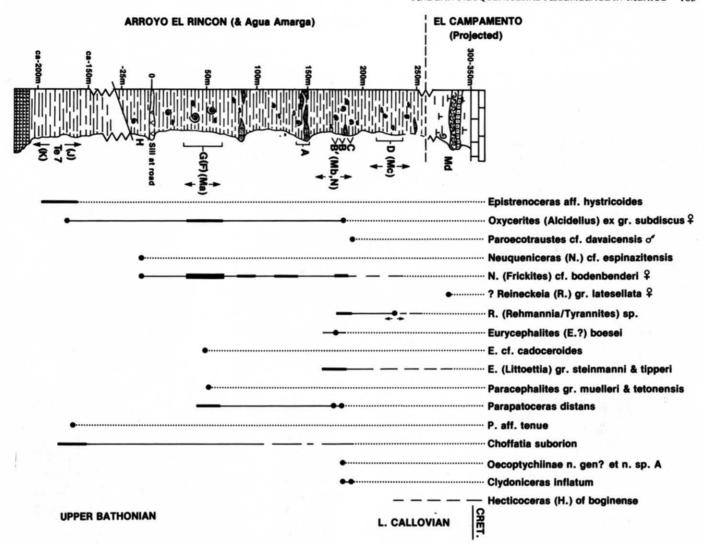


Figure 2. Columnar section of the Yucuñuti Formation at Coauilote with ammonoid occurrances, based on our new findings at the localities indicated in Figure 1. Dots indicate single occurrances.

from the ?Middle Callovian of Chacay Melehue differ in the somewhat wider umbilicus.

Clydoniceras inflatum Westermann n.sp., & (Pl. I, Fig. 2a-c; Pl. III, Figs. 6, 7). This species is known in several specimens from levels B and C of the El Rincon section of which the figured specimen is the holotype, 2 specimens from bed B of the

El Campamento section, and in several loose specimens. The diagnostic character is the involute, inflated, and bisulcate shell with prominent ribbing. The species is, in fact, homeomorphic with the Lower Bajocian sonniniid Poecilomorphus except for the septal suture which is even simplier (i.e., with two-pronged lateral lobe and multiple, small umbilical elements typical of

EXPLANATION OF PLATE I

Figures 1 a,b. Oxycerites (Paroxycerites) ex gr. subdiscus (d'Orbigny); lateral and ventral views; McMaster J 2109a, middle part of Yucuñuti Formation, locality F, N.W. of Coauilote. (X 0.9).

Figures 2a-c. Clydoniceras inflatum Westermann n.sp., holotype, lateral and ventral views of incomplete specimen; McMaster J 2110a, middle part of Yucuñuti Formation, level B of El Rincon section. (X 1.5). (See also Pl. III)

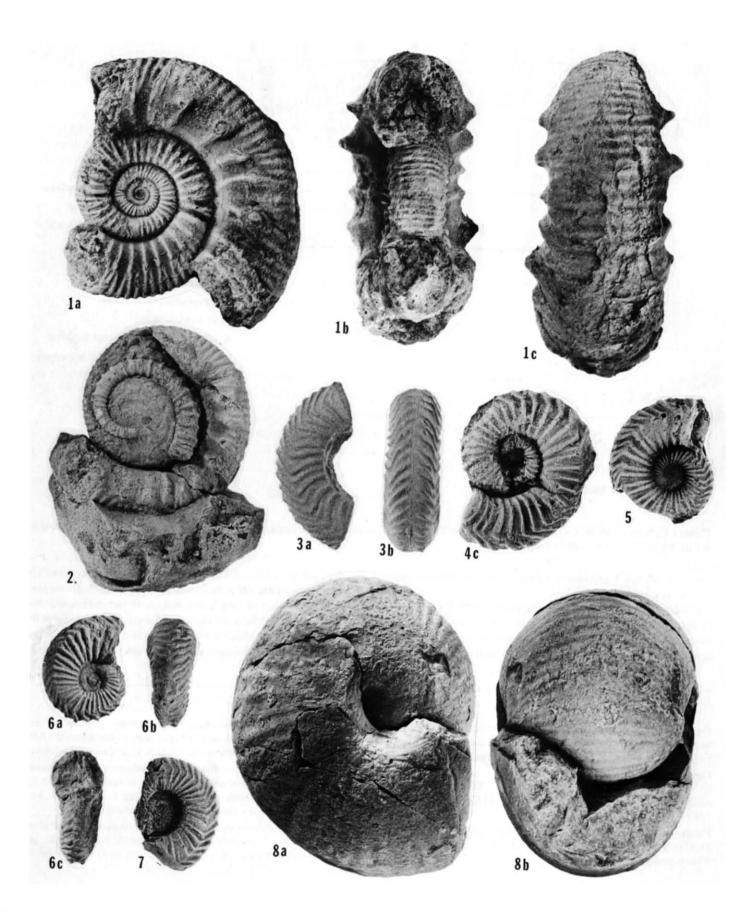
Figures 3a-c. Oecoptychiinae n.sp. A, lateral and ventral views; McMaster J 2110b, middle part of Yucuñuti Formation, level B of El Rincon section. (X 1.5).

Figures 4 a,b. Neuqueniceras (Neuqueniceras) sp. 3, lateral and ventral views of almost complete microconch; McMaster J 1209b, middle Yucuñuti Formation, locality F, N.W. of Coauilote. (X 0.9).

Figures 5 a,b. Neuqueniceras (Neuqueniceras?) cf. "neogaeum" (Burckhardt) Q, lateral and ventral views of macroconch with 1/2 whorl incomplete body chamber; McMaster J 2119a, loose from Yucuñuti Formation, Coauilote (purchase Corona). (X 1).

Figures 6 a,b. Reineckeia (Rehmannia /? Tyrannites) sp. Q, lateral and ventral views of entirely septate macroconch; McMaster J2114a, upper part of Yucuñuti Formation, level D of El Rincon section. (X 1).

PLATE II



clydoniceratids). Some specimens are septate up to 52 mm in diameter (Pl. III, Figs. 7a,b) while body chamber fragments indicate only 40 to 55 mm maximum size. They show no reduction in the raised ventral shoulders defining the ventral furrows, nor in the secondary ribbing. These body chambers appear therefore to be the microconchs of Cydoniceras, i.e., "Delecticeras" (cf. Westermann, 1956). This species is much more inflated, particularly ventrally, than any known species of Clydoniceras, macroconch or microconch, and has more prominent and more flexed ribbing. The known range of Clydoniceras is from late Middle to latest Bathonian of western Europe, north Africa, Madagascar and Baluchistan. Bisulcate forms, however, are known only from the "Aspidoides" Zone (recte Orbis Zone) and Discus Zone of Europe (Callomon, pers. commun.; cf. Dietl, 1982) and from Madagascar (Collignon, 1958).

Hecticoceras. The single specimen of H. (Hecticoceras) cf. boginense Petitclerc of the H. hecticum group (Pl. III, Figs. 9 a-c) from the upper part of the El Campamento section, appears to be the first find of Hecticoceratinae in North America (specimen identified by S. Elmi and E. Cariou, pers. commun.; cf. Elmi, 1967, Pl. II). The only other known eastern Pacific occurrence of this important Tethyan subfamily is in the Neuquén Basin, Argentina (Stehn, 1923; Westermann, 1981). The specimen was found loose at level Mc and according to surface gradient, strike and dip, must have been derived from above. The matrix of yellow mudstone resembled that of level M near the top of the section. The somewhat distorted body chamber has a compresses subrectangular whorl section with blunt ventral fastigation and tuberculate dichotomous ribbing. This form is restricted to the uppermost Lower Callovian, Proximum Horizon and Patina Subzone of the Gracilis Zone (Cariou, 1980) and abounds in the western Subtethyan province (Elmi and Cariou, pers. commun.).

Family Sphaeroceratidae

Eurycephalites, Lilloettia, and Xenocephalites. The subfamily Eurycephalitinae Thierry and its Andean taxa are currently being revised by Riccardi and Westermann. We follow Callomon (in Donovan et al., 1981) in classifying the macrocepha-

litins as a subfamily of the Sphaeroceratidae. Lilloettia is placed as a subgenus in Eurycephalites.

Eurycephalites (E.?) boesei (Burckhardt) ♀ was probably based on the single, figured body chamber from the Cualac area which is therefore the holotype. (A second specimen in the old collection of the Instituto de Geologia is unlabelled and was apparently not available to Burckhardt.) This macroconch is intermediate in size, whorl shape, and ornamentation between the typically small nominate subgenus with subquadrate and rather ornate whorls and the typically large subgenus Lilloettia with ovate to subtriangular and more finely ornate whorls. We have single specimens from? level B of the El Rincon section and from the approximately equivalent level C of the El Huizache section 4 km north of Tecocovunca (Pl. III, Fig. 3). At both localities, the species is associated with a more compressed and finer ribbed form with even more reduced primaries, closely resembling E. (Lilloettia) tipperi Frebold (Pl. III, Figs. 1a,b) [= "Macrocephalites aff. macrocephalus" of Burckhardt 1927, Pl. 16, Figs. 1-3]. Callomon (this volume) suggests that E. boesei may be conspecific with the North-Cordilleran E. buckmani (Crickmay), and furthermore, E. lilloetensis Crickmay (including L. mertenyarwoodi Crickmay) and E. buckmani Crickmay may be mere variants of the same species. Crickmay's and Frebold's North-Cordilleran species were originally described from isolated outcrops in southern British Columbia; only the E. lilloetensis-buckmani association can now be dated as clearly early Callovian from occurrances above the Cadoceras range zone in South Alaska (Imlay, 1953; Callomon, this volume). According to the plastercasts available to me, E. tipperi has consistently smooth inner flanks on the internal mould, at least as far back as 25 mm diameter while the inner whorls at a similar diameter to E. lilloetensis on the holotype and on the dated specimens illustrated by Imlay (1953b, Pl. 30) from the Chinitna Formation of southern Alaska, have well developed primaries at the same growth stage. Similarly, the specimens of E.(L.) buckmani from the Chinitna, illustrated by Imlay (Pl. 27) are partly from the same beds as E. lilloetensis, and are much more coarsely ribbed on the flank than the Mexican topotypes of E. boesei found together with E. gr. steinmanni and tipperi. Thus I conclude that the two Cualac forms mentioned, on the one hand, and the North-Cordilleran

EXPLANATION OF PLATE II

Figures 1a-c. Neuqueniceras (Frickites) cf. bodenbenderi (Tornquist), lateral and ventral views of entirely septate macroconch; McMaster J 2160a, middle part of Yucuñuti Formation, locality F, N.W. of Tecocoyunca. (X 0.85).

Figure 2. Parapatoceras cf. distans (d'Orbigny), in umbilicus of Neuqueniceras sp., lateral view of incomplete specimen; McMaster J 2110a, from middle part of Yucuñuti Formation, level B of El Rincon section. (X 1).

Figures 3-7. Epistrenoceras aff. hystricoides Rollier, XI. 3a,b) the holotype of Cosmoceras paracontrarium Burkhardt, (nomen dubium), lateral views of somewhat crushed and incomplete body chamber;

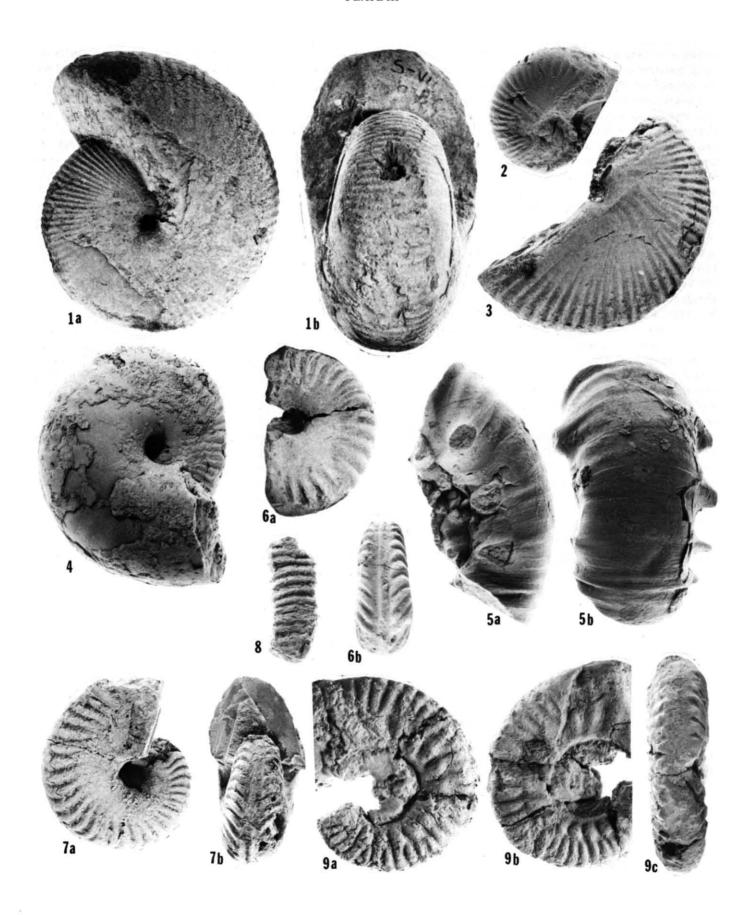
Inst. Geol. Mex., lower part of Yuruñuti Formation, area of Cualac (?Coauilote-Tecocoyunca).

4) lateral view of almost complete, coarsely ribbed specimen; McMaster J 2108b, loose from (lower part of) Yucuñuti Formation, Coauilote. 5-6c) lateral and ventral views of entirely septate specimens, with spinose intermediate stages; McMaster J 2108c-d, loose from (lower part of) Yucuñuti Formation, Cuaolote. (X 1).

7) lateral view of small, almost complete specimen with 1/2 whorl body chamber, ? microconch; McMaster J 2108e, loose from (lower part of) Yucuñuti Formation, Coauilote. (X 1).

Figures 8 a,b. Bullatimorphites (Kheraiceras) bullatus (d'Orbigny) ♀, lateral and ventral views of almost complete macroconch; McMaster J 2108a, loose from Yucuñuti Formation, Coauilote. (X 1).

PLATE III



forms, on the other, may respectively be variants of single species as suggested by Callomon, but that the Mexican species is not conspecific with the North-Cordilleran species. A single minute E. (Lilloettia?) sp. indet. juv.(?) (Pl. III., Fig. 3), however, has been found as high as the top of the Yucuñuti Formation (level Md of El Campamento section).

In the Andean Province, E. (L.) steinmanni Spath closely resembles our compressed form. It occurs in the lower part of the Cemetery section at Caracoles, Chile (beds 2-3) below Neuqueniceras (Frickites) and together with E. aff. boesei (Westermann, 1967), and in the upper part of the thick shaley section of Chacay Melehue (McM. J 1204), Neuquén (bed 4) mainly above Neuqueniceras s.s. and together with E. (Imlayoceras?) cf. cadoceroides (Burckhardt) (Riccardi and Westermann, unpublished). Significantly, the same bed 2 at Caracoles also contains rare Prohecticoceras cf. ochraceum Elmi, Q and ∂ (unpublished), a species known previously only from the Lower to lower Upper Bathonian of western Mediterranean and Poland (Elmi, 1967, 1971).

Eurycephalites (Imlayoceras?) cadoceroides (Burckhardt), based on the monotypic holotype supposedly from Mixtepec in northwest Oaxaca, also occurs at Coauilote in the middle part of the El Rincon section (ca. our level G) according to our inspection of Erben's collection Te 6. Imlayoceras Frebold is, however, based on a single isolate fauna from Alberta and could merely be an extremely inflated Lilloettia or Iniskinites (Callomon, this volume; Riccardi and Westermann, unpublished).

The rare microconchiate Xenocephalites nikitini (Burckhardt, 1927; Pl. XVI, Figs. 8, 9 here designated the neotype, holotype Figs. 4-7 lost) resembles X. vicarius, X. hebetus, and X. hartsocki Imlay spp. from South Alaska where they belong to the late Bathonian and Early Callovian Iniskinites and Lilloettia faunas (B5-B8 of Callomon, this volume). The microconchs, however, show much smaller interspecific variation than the macroconchs and cannot be dated as precisely as the macroconch (Callomon, this volume and pers. commun.). Another closely affiliated species is X. gottschei (Tornquist) from the Neuqueniceras (Frickites) assemblage of the? basal Callovian of the southern Andes. X. cf. phillipsi Imlay, originally described from Montana (fauna A8 of Callomon, this volume) and X. "herrero-duclouxi" Stipanici (1966), a relative of X. neuquensis Stehn from Neuquén, occur at unknown levels also at Coauilote. Unfortunately, all Eurycephalitinae are relatively rare in Mexico so that their ranges are difficult to establish.

Of particular interest is also the probable occurrence in the Neuqueniceras assemblage north of Coauilote of Paracephalites gr. muelleri and tetonesis (Imlay) Q (Pl. III, Fig. 4), another East-Pacific Eurcephalitinae genus hitherto known only from the Upper Bathonian of the Western Interior United States (Imlay 1955a; faunas A5, 6 of Callomon, this volume). It is even possible that the ex situ? Xenocephalites cf. "herrero-declouxi" ♂ mentioned above is the matching microconch, i.e., X.? shoshonense (Imlay, 1953a; Callomon, this volume). Closely similar Eurycephalitinae species also occur in southern Peru (Westermann et al., 1980).

Family Perisphinctidae

Choffatia. The genus is understood conservatively to include Subgrossouvria, Parachoffatia and Homoeoplanulites. C. suborion (Burckhardt, 1927; lectotype here designated Pl. XXXI, Figs. 2-4, 104 mm diameter; ? synon. "Perisphinctes" cualacensis Burckhardt, 1927) occurs at an unknown level at Cuauilote. An identical form occurs in the Neuquén Basin at Chacay Melehue, and perhaps at Caracoles (? "P." gottschei Steinmann); similar species also abound around the Bathonian/Callovian boundary of Europe. Forms reminiscent of the Andean C.? gleimi (Steinmann), C. jupiter (Steinmann), and C.? pseudoeuryptycha (Tornquist) also occur at Cuauilote, but cannot yet be clearly identified.

Family Perisphinctidae or Reineckeiidae

?Neuqueniceras. Of particular interest are several small forms of Burckhardt (1927), i.e., "Perisphinctes" weitzi and "Peltoce-

EXPLANATION OF PLATE III

Figure 1. Eurycephalites (Lilloettia) ex gr. steinmanni Spath and tipperi Frebold Q, lateral and ventral views of mostly septate macroconch; McMaster J 2121, upper third of Yucuñuti Formation, level C of El Huizache section, N. of Tecocoyunca. (X 1.1).

Figure 2. Eurycephalites (Lilloettia?) sp. indet. juv.(?), body chamber and mostly destroyed phragmocone; McMaster J 2122, top of Yucuñuti Formation, level Md of El Campamento section. (X 1.5).

Figure 3. Eurycephalites (E.?) boesei (Burckhardt) Q, body chamber body chamber and incomplete phragmocone; McMaster J 23123, upper part of Yucuñuti Formation, level C of El Huizache section. (X 1).

Figure 4. ?Paracephalites ex gr. muelleri and tatonensis Imlay Q, lateral view of almost complete specimen; McMaster J 2127, middle part of Yucuñuti Formation, near Tecocyunca. (X 1).

Figures 5 a,b. Reineckeia (Reineckeia?) sp. indet. ["No. 2" of Burckhardt, 1927], lateral and ventral views of fragment from last 3 whorls, including body chamber; McMaster J 2126, top of Yucuñuti Formation, level Md of El Campamento section. (X 1).

Figures 6-7. Clydoniceras inflatum Westermann n.sp., Yucuñuti Formation, ex situ near Coauilote. (Approximately X 1).

6 a,b) lateral and ventral views of small body chamber, microconch; McMaster J 2124,

7 a,b) lateral and ventral views of large phragmocone, septate; McMaster J 2125. (See Pl. I)

Figure 8. Fragment of ? Parapatoceras aff. tenue (Baugier and Sauzé) (?or a re-worked Late Bajocian Spiroceras annulatum (Desh.)), lateral view of fragment; McMaster J 2129, from the lower part of the Yucuñuti Formation, Epistrenoceras level, basal part of Agua Amarga section, Coauilote. (X 1).

Figures 9 a-c. Hecticoceras (Hecticoceras) cf. boginense Petitclerc, both lateral views and ventral view of body chamber with end of phragmocone; McMaster J 2128, at or near top of Yucuñuti Formation ex situ, levels c-d of El Campamento section. (X 1).

ras" constrictum, which appear to be intermediate between Perisphinctidae and Reineckeiidae and resemble the inner whorls of Neuqueniceras (Frickites) cf. bodenbenderi (Tornquist) ♀ as described below. "P." weitzi also resembles the "Simoceras sp." from Espinacito Pass, Argentina, described by Gottsche (1878, Pl. III, Figs. 5a-b), while "P." constrictum is close to "Perisphinctes" boehmi (Steinmann) from Caracoles, Chile.

Family Reineckeiidae

Neuqueniceras. Current investigations at the Argentine type localities of Neuqueniceras spp. (Chacay Melehue, Neuquén province) and of the subgenus Frickites (Espinacito Pass, San Juan province) by Riccardi and Westermann, indicate that the two taxa are intimately related through transitional forms. Their distinction at the generic level was recently upheld, however, by Cariou (1980) who also erected the new subfamily Neuqueniceratinae. The group including the type species N. steinmanni (Stehn), all possibly belonging to a single variable species, is characterized by the small to medium-sized macroconchs bearing blade-like primaries on the entire phragmocone and a more or less distinct ventral costal interruption, while the body chamber has prominent mid-lateral to ventro-lateral bullae which usually bear spines. The group including the type species of N. (Frickites) bodenbenderi (Tornquist) has large macroconchs with a similar "perisphinctid" juvenile stage followed by an intermediate growth stage bearing moderately short primaries with mid-lateral turbercles and an outer stage of approximately two whorls developing very prominent and conical mid-lateral spines; the mid-ventral interruption is only faint and irregularly developed (obsolescent) intraspecifically and morphogenetically. The inner whorls of the macroconch and the poorly known microconch of N. (Frickites) cf. bodenbenderi from Cualac thus tend to resemble Burckhardt's "Perisphinctes" weitzi, with perisphinctid ribbing except for the tiny mid-lateral tubercles. Because of the difficulty of placing many specimens (and "species") into either taxon, Neuqueniceras and Frickites are distinguished here at the subgeneric level only. By what appears to be phyletic acceleration of development, i.e., palingenetic reduction of the juvenile perisphinctid stage and its progressive replacement by the reineckeiid stage, N. (Frickites) seems to have developed into the early subgenera Rehmannia and Tyrannites (Cariou, 1980) of Reineckeia, which we believe are present in the upper third of the Coauilote section (Fig. 2).

Neuqueniceras s.s. is probably represented in Mexico by "Peltoceras neogaeum" Burckhardt (1927, Pl. II, Figs. 4,5) which, unfortunately, is based on a single very fragmentary and partly crushed psecimen, i.e., the holotype, from the Cualac area. Even the plastotype does not permit safe identification of topotypes so that the specific name should be considered a nomen dubium. Similarly, the seemingly very close "Peltoceras monacanthum" Burckhardt is based on fragments of a single specimen from an unknown stratigraphic level at the old El Consuelo coal mine in NW Oaxaca province, and the important septate fragments have been lost. These forms are known from Coauilote only in rare, unlocated specimens. "P. neogaeum" has also been recorded from localities in Northwest Oaxaca, e.g., Yucuñuti, as well as from the Huayacocotla Mountains in east-central Mexico (Erben, 1956; Cantu Chapa, 1979; cf. Taylor et al., this volume).

The subgenus Frickites is represented by the most abundant species in the highly fossiliferous middle part of the Yucuñuti Formation at Coauilote-Tecocoyunca, but apparently was not described in Burckhardt's monograph on Cualac. N.(F.) cf. bodenbenderi (Tornquist) (Pl. II, Figs. 1a-c) is very close to the Andean species from Espinacito Pass, San Juan province, and partly indistinguishable from Caracoles material above the Lilloettia beds (Cemetery section, beds 5, 8). The only possible difference may be in the even less developed mid-ventral interruption which is generally considered as a highly variable feature of low taxonomic value. The fossiliferous levels at Coauilote (El Rincon G/F, El Campamento Ma) also contain a large strongly depressed form resembling Reineckeia aberrans Burckhardt. This species is also poorly founded on an originally incomplete holotype only - part of which is lost. The remaining fragments resemble the highly ornate Andean N.(F.) antipodum (Gottsche) from Espinacito Pass and the closely similar N.(F.)euactis (Steinmann) from Caracoles and also extremely depressed Choffatia. The affinity of "Reineckeia" plicata Burckhardt is also poorly known because the holotype, the only specimen originally placed in that taxon, is lost.

According to the recent monograph by Cariou (1980), the Tethyan Reineckeiinae evolved from Choffatia (Homoeoplanulites) in the upper Macrocephalus Zone leading to Rehmannia and Reineckeia (Tyrannites). Both are said to have "perisphinctoid" inner whorls with minute tubercles only, followed by the outer coronate reineckeiid stages. R. (Tyrannites) is said to be distinguished from Rehmannia by the appearance of a reineckeiid stage already on the mature phragmocone, while it is restricted to the body chamber in the latter. Dr. Carious has kindly sent us a plastotype of R. (Tyrannites) franconica. It is almost indistinguishable from specimens from beds B to D in the upper part of the El Rincon section (Pl. I, Figs. 6a,b). Other Coauilote forms are very close to Rehmannia rehmanni (Oppel) and R. (R.) grossouvrei (Petitclerc), apparently the earliest known Tethyan reineckeiids. We thus consider the taxa Tyrannites and Rehmannia as closely interrelated and prefer to place both as subgenera, or as one subgenus, in the genus Reineckeia. All species are said to be restricted to the Lower Callovian (Cariou, 1980).

Reineckeia s.s. has now been tentatively identified from the uppermost Yucuñuti Formation in the El Campamanto section, i.e., ?R.(R.) ex. gr. latesellata Burckhardt and "Reineckeia sp. indet. 2" of Burckhardt (1927, Pl. 21). Both forms were originally described from the long abandoned El Consuelo coal mine, northwest Oaxaca. The majority of the 20-odd Reineckeia "species" described by Burckhardt from that locality, including S. [Erymnoceras auct.] mixtecorum, all with coronate inner and outer whorls, could belong to but a single species; R. latesellata represented the best material. Our specimen is mostly septate and is coronate at least as far back as the earliest preserved whorl at ca. 15 mm in diameter. The large fragment of "R.? sp. indet. 2" of Burckhardt (Pl. III, Figs. 5a,b) bears distant prominant spines on all of the three last whorls preserved. Reineckeia s.s. is said to range from the topmost Lower to the lower Upper Callovian (Cariou, 1980).

Family Tulitidae

Bullatimorphites. The circum-global Tethyan subgenus Bullatimorphites (Kheraiceras) is represented by the similarly widespread species B. (K.) bullatus (d'Orbigny) s.l. Our single macroconch (Pl. II, Fig. 8a,b) probably came from the basal or middle Yucuñuti Formation. It was found loose and said to have come from locality J. The monotypic holotype, now lost, of B. (K.) v-costatus (Burckhardt) from the Cualac area differs only in the curved secondaries on the intermediate whorls forming blunt obtuse ventral chevrons. Erben (1956, p. 121) recorded this species from the Otatera or basal Yucuñuti Formation of Tezoquio, but the specimen is lost. Although one cannot decide from such single specimens whether this difference is intra-or inter-specific, the same two forms occur again at Caracoles, Chile (beds 3-5 of the Cemetery section).

Our specimen of B. bullatus Q is fully grown and almost complete. The ribbing on the body chamber becomes obsolete at about 70 mm diameter and the complete diameter is estimated at only approximately 85 mm. The number of secondaries on the penultimate half-whorl is 25. This agrees more closely with the mainly Lower Callovian B. bullatus s.s. than with the mainly Upper Bathonian B. bullatus hannoveranus (Roemer), which differs in larger size and coarser ornament (Gabilly, 1964; Westermann, 1958). An inspection of Gabilly's large collections from western France, however, showed that these chrono-subspecies (or transients sensu gallico) have appreciable morphologic overlap. Furthermore, both forms are said to have similar ranges in southern Germany (Hahn, 1971) so that their stratigraphic usefulness is limited.

?Family Tulitidae

Oecoptychiinae. A single small specimen from bed B of the El Rincon section (Pl. I, Fig. 3a-c) is identified only with Oecoptychiinae n.sp. A. It has the characteristic geniculate body chamber of Oecoptychius, a micromorph genus known only from the (? entire) Callovian (and? Oxfordian) of western Europe. Our specimen differs, however, in the absence of the mid-ventral interruption and backward curvature of the costae that are consistently present in the European genus. Our specimen resembles the Bullatimorphites microconchs Bomburites and Treptoceras in all features but the extremely small size and the strong geniculation and appears thus to be intermediate between Bullatimorphites & and Oecoptychius in morphology and age. This supports Schindewolf's (1965) opinion which tentatively placed th Oecoptychiinae Westermann in the Tulitidae, and also is consistent with the original analysis of the sutural ontogeny (Westermann, 1956). On the other hand the recent classification by Callomon (in Donovan et al., 1981) includes Oecoptychius in the Strigoceratidae of the Haplocerataceae. Significantly, the appearance of Oecoptychius in Europe is cryptogenic and the closest possible known ancestor in Europe seems to be the middle Bathonian tulitid Sphaeroptychius (cf. Enay, 1959).

?Family Spiroceratidae

Parapatoceras. The species Parapatoceras distans (d'Orbigny) from Coualote has been described previously under the

name of Infrapatoceras biserratum Ochoterena, gen. et sp. nov. (1966) based on Erben's collection from locality Te 3. Infrapatoceras was said to be distinguished from Parapatoceras, a well-known late Bathonian to early Callovian genus found in western Europe, Oregon and Chile, by the somewhat simpler septal suture; L and U are without frilling, I rounded - features which today are not considered to be of taxonomic significance at the genus-level (Dietl, 1978; Donovan et al., 1981). In fact the Mexican species (Pl. II, Fig. 2) may not be distinct from the European Late Bathonian to Early Callovian P. distans which, according to Hillebrandt (1973, p. 174) and our field work, also occurs in the Sierra Domeyko of N. Chile.

From the Epistrenoceras beds of the Agua Amarga section comes a single fragment (Pl. III. Fig. 8) which resembles Parapatoceras tenue (Baugier and Sauzé) as recently re-described by Dietl (1978, p. 44, Pl. 7, Fig. 10). Our specimen differs in the somewhat more prominent and less strongly oblique ribs, although that perhaps could be due to the slight distortion. Significantly, P. tenue is known mainly from the Upper Bathonian of northern Chile where it is associated with P. distans, but very rare in the Upper Bathonian of France and Switzerland (Dietl, 1978). There is, however, also the possibility that our fragment is a re-worked Late Bajocian Spiroceras annulatum (Desh.), i.e., from the Taberna Formation also present in the area; there is close resemblance in the prominence and weak obliquity of the ribs (cf. Dietl, 1978, Pl. 6, 7).

Epistrenoceras. The holotype of Epistrenoceras paracontrarium (Burckhardt, 1927), the only specimen originally described from the "basal beds of the upper Dogger" of Cuauilote at Cualac, is too incomplete for interpretation of the species (Pl. II, Figs. 3a,b). The present sample includes several almost complete specimens (Pl. II, Fig. 4). The author said that the holotype was different from the European E. contrarium (d'Orbigny, 1842-1849, Pl. 145, Figs. 1, 2 only) from the Upper Bathonian of Niort, northern France, because the whorl was more inflated with maximum width near mid-flank and because of the lower position of the inflexion point of the ribs, i.e., at mid-flank instead of the upper third. According to d'Orbigny's illustration (which may not be reliable), E. contrarium has large evolute septate whorls and isocostate, moderately coarse ribbing with ventrolateral bullae. Our well preserved topotypes of E. paracontrarium show, however, that the supposed differences of whorl section and ornament are due partly to the lateral crushing of the holotype of E. paracontrarium and partly to the slightly variocostate modification of the body chamber; the geniculate inflexion is at about 3/5 whorl height as in the European form, while the section varies from subcircular to ovate with maximal whorl width usually at about 2/5 height. Our septate specimens, 30 to 35 mm diameter, are all much more involute than d'Orbigny's illustration and most have typically variocostate secondaries. In some, the penultimate septate half-whorl of about 20 mm diameter has distant ventrolateral spines which discontinue abruptly on the ultimate halfwhorl and change into dense secondaries ending in blunt nodes (Pl. II, Figs. 6a-c). On other specimens, the spinose stage continues to the body chamber. On one incomplete body chamber of 35 mm in diameter, the primaries shorten with the inflexion moving to mid-flank, thus resembling the holotype.

The narrow umbilicus and the presence of prominent ventrolateral spines at some stage in the majority of our Cualac specimens indicate close affinity to the Upper Bathonian *E. hystricoides* Rollier (for d'Orbigny, 1842-1849, Pl. 145, Figs. 3, 4) from western Europe except that the ribbing is denser than in d'Orbigny's illustration.

The holotype of *Cosmoceras paracontrarium* may thus belong to either species. Most topotypes sway the balance toward *E. hystricoides* but this must remain uncertain because its type lacks the entire phragmocone.

One specimen (Pl. II, Fig. 8) appears to be fully grown at 30 mm in diameter. It has a much more compressed body chamber than the larger specimens and has ventrolateral bullae of medium strength persisting to the end. This is either another species or possibly the (matching) microconch of the form described above.

Of the 20 specimens of *Epistrenoceras* available to us, we collected 7 from beds with yellow siltstone and marl, together with the bivalves *Vaugonia, Anisocardia* and *Unicardium* and the ammonite *Choffatia*, in the lowest part of the Agua Amarga section, Coauilote (ca. locality J), and one at locality K.

E. paracontrarium was reported together with Prohecticoceras from Sierre Domeyko in northern Chile (Hillebrandt, 1973), but the specific identification needs confirmation.

AGE AND DISTRIBUTION OF THE NEUQUENICERAS ASSEMBLAGE

This moderately diverse assemblage occurs in great abundance through 30 to 35 m (interval G/F) of shales in the middle of the Yucuñuti Formation at Caouilote (Fig. 2). It includes the dominant Neuqueniceras (Frickites) cf. bodenbenderi (Tornquist), the somewhat less common N.(F.)? aff. aberrans (Burckhardt) and Ptychophylloceras plasticum (Burckhardt), and the accessories Eurycephalites (s.s. +? Lilloetia) spp., Choffatia sp., Oxycerites (Paroxycerites) gr. subdiscus (d'Orbigny) and Parapatoceras distans (Baugier and Sauzé). This interval was presumably also the principal source of Burckhardt's type specimens. The entire range of genus Neuqueniceras is, however, through at least 200 m of the Caouilote section (levels H to B), while the ranges of most of the other taxa cannot yet be established because of relative scarcity outside the interval G/F. There has been, to our knowledge, no evidence for positioning the Neuqueniceras assemblages above an assemblage of Eurycephalites boesei (Burckhardt) and Xenocephalites as recently tabulated by Imlay (1980, Fig. 14), nor for his dating of this (and his lower) assemblage as (late) Early Callovian following previous authors (Burckhardt, 1927, 1930, Erben, 1956). On the other hand, we now confirm the stratigraphic position of the Neuqueniceras assemblage above the mid-Late Bathonian Epistrenoceras.

The lower ca. 200 m of the Yucuñuti Formation (below bed H near the reference level in Figs. 1, 2) as well as the probably coeval beds outcropping east of Coauilote have yielded to us neither *Neuqueniceras* nor *Eurycephalites*. Near the base we found, however, a single *Epistrenoceras* aff. *hystricoides* (Rollier) (locs. J, K) together with *Choffatia suborion* and an

abundant bivalve and locally, brachiopod fauna. This is at approximately the same level as Erben's locality Te 7 near Tecocoyunca from which he recorded Epistrenoceras paracontrarium. In the better documented sections in Mediterranean and Submediterranean Europe, the range of Epistrenoceras is apparently restricted to the middle Upper Bathonian, i.e., the Retrocostatum Zone auct., recte Aspidoides Standard Zone (Torrens, 1980), most recently renamed the Orbis Zone (Dietl, 1982). The relative scarcity in Mexico of ammonites in these lower beds yielding, in part, abundant bivalves and brachiopods, is presumably due to ecologic conditions unfavorable to ammonites, so that the first appearance of the Neuqueniceras-Eurycephalites fauna may be diachronous. This sequence, the first reineckeiids following well above Epistrenoceras, is nevertheless the same as in northern Chile and (?) southern Peru (Hillebrandt, 1970 and pers. commun.; Westermann et al., 1980).

The age of the upper range limit of the Neuqueniceras assemblage is now suggested by the first circum-Pacific find of Clydoniceras, i.e., C. inflatum n.sp., at levels B and C of the El Rincon section and the approximately equivalent level Mb of the El Campamento section (Fig. 2). In the better documented European sections, bisulcate Clydoniceras species are limited to the middle and upper Upper Bathonian, i.e., Orbis and Discus Zones, and the family became extinct. However, this does not preclude survival elsewhere.

Level B of El Rincon has also yielded representatives of what seemed to be the earliest tue Reineckeia, i.e., subgenus Rehmannia (and/or Tyrannites), which in the Tethys appears only in the upper Macrocephalus Zone, Rehmanni Subzone, of the Lower Callovian (Cariou, 1980). At this level Eurycephalites (Lilloettia) ex gr. tipperi Frebold and steinmanni Spath as well as E.(E.?) boesei Burckhardt also occur. The very closely affiliated or conspecific E. (L.) steinmanni Spath of the Andean Province occurs at Caracoles (below Neuqueniceras!) together with Prohectiococeras cf. ochracensis Elmi, a West-Tethyan species known only from the Bathonian up to the Hodsoni (or ?Orbis) Zone. The Late Bathonian, rather than Early Callovian, age of the Neuqueniceras assemblage is also supported by the first Mexican find of ?Paracephalites ex. gr. muelleri and tetonensis Imlay hitherto known only from the Upper Bathonian of the Western Interior, United States (Callomon, this volume). The tentative age of the Neuqueniceras assemblage is latest Bathonian to (?) earliest Callovian.

The Clydoniceras inflatus assemblage (El Rincon levels B, C) lies approximately at the Bathonian/Callovian boundary so that the first appearance of Reineckeia (Rehmannia/Tyrannites) sp. appears to be here slightly earlier than in the Mediterranean Province. This and the apparent morphological intergradation into Neuqueniceras (Frickites) ex. gr. bodenbenderi suggest an East-Pacific, rather than Mediterranean, origin of the Reineckeiidae.

Latest Lower Callovian age is evident for the uppermost Yucuñuti Formation (El Campamento section) by the first find of the *Hecticoceras* (*Hecticoceras*) cf. *boginense* Petitclerc, hitherto known from the West-Tethyan uppermost Lower Callovian (Elmi, pers. commun.). ? *Reineckeia* (*Reineckeia*) ex gr.

latesellata Burckhardt even suggests Middle to Upper Callovian. Rare probable Eurycephalites (Lilloettia?) sp. also ranges up into the topmost Yucuñuti Formation (level Md).

PALEOBIOGEOGRAPHY

The exceptionally close taxonomic affinity of the Neuqueniceras assemblage of Cualac to the Andean fauna of Chile and Argentina has been discussed elsewhere by me in this volume (Taylor et al). At least half and possibly two-thirds of the ammonite species appear to be in common with the rich faunas of Caracoles in Antofagasta province, Chacay Melehue in Neuquén province, Passo del Espinacito in San Juan province, the Sierra Domeyko in Antofasgasta province (collected by von Hillebrandt), and probably southern Peru. This Andean assemblage overlies beds with Epistrenoceras as in Mexico, while Hecticoceras and true Reineckeia occur at a higher level. Such a close faunistic affinity is compatible with the recent plate-tectonic hypothesis, that the Mixteca terrane (northeast Guerrero and northwest Oataca states) carrying the Neuqueniceras assemblage is allochthonous with respect to the North American craton (Coney and Campa, 1983).

Parts of the Neuqueniceras assemblage, e.g., Neuqueniceras neogaeum (Burckhardt), were also reported from the Tepexic Formation of the Huayacocotla Mountains in the Sierra Madra Oriental, east-central Mexico (Erben, 1956; Cantu Chapa, 1979 and earlier). The old material, however, is either lost or unavailable for confirmation and recently one of us (Westermann) was unable to duplicate the findings (see Taylor et al., this volume).

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