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PERUNAUTILUS QUADRATUS N. GEN. ET SP. (CEPHALOPODA, NAUTILIDA) FROM THE TRIASSIC (NORIAN) OF CENTRAL PERU

BY

REX E. CRICK and E. S. SOBOLEV

With 1 plate and 3 text-figures

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Summary

The new genus and species *Perunautilus quadratus* (Cephalopoda, Nautilida, Liroceratidae) is described from Triassic (Norian) strata of central Peru. The general details of the stratigraphic distribution of family Liroceratidae is presented together with specific details of the stratigraphic and geographic distribution of Triassic species. The biogeographic implications of this occurrence are discussed in the context of the family and Triassic paleogeography.

Key words: Cephalopoda – Nautilida – Peru – Triassic – taxonomy – biogeography.

Contents

Introduction

Nautilid cephalopods of Norian age are poorly known globally to the point of being exceedingly rare (Kummel 1953, Moore 1964), particularly from South America. Perhaps the best known Norian cephalopod faunas have been described from the northeastern regions of Siberia (Sobolev 1989). Because of this rather meager record and the similarity of *Perunautilus* n. gen. with *Tomponautilus* (Siberia), the occurrence of this genus and species in Peru provides new information about the dispersal characteristics of the Liroceratidae and extends the distribution of the family into the southern mid-paleolatitudes along the western edge of Pangaea.

Material and methods

The material described and illustrated here was provided by G. D. Stanley who, in an earlier contribution in this volume, provides background on the geology, stratigraphy and geography of the region. The three

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illustrated specimens came from a zone low in the Chambara Formation at Shalypayco, Peru. Fragmentary specimens from a section near Huanincocha, though silicified, were not sufficiently complete to allow positive placement in the new genus and species.

Several of the descriptive terms or their meaning as used here have been adapted or adopted from the work of SOBOLEV (1989) and published in Russian. The following are summarized here in English to facilitate their use in this work and others to follow.

Siphuncle diameter. The diameter of the siphuncle relative to the dorso-ventral diameter of the phragmocone is a recognized measure of taxonomic affinities at several taxonomic levels because of its relationship to the physiology of the animal. And while this ratio has often been quantified in one form or another, SOBOLEV (1989) has made a consistent practice of segregating these ratios into categories for nautilids. These categories are based on the ratio Ds/Hw where Ds is the diameter of the siphuncle at the foramen and Hw is the whorl height measured in the dorso-ventral plane and identified as: agastenosiphonate (> 0.0 to 0.03); stenosiphonate (> 0.03 to 0.13); mesosiphonate (> 0.13 to 0.17); eurysiphonate (> 0.17). The terms stenosiphonate and eurysiphonate were standardized in the "Treatise of Invertebrate Paleontology – Part K" (MOORE 1964). Agastenosiphonate and mesosiphonate are introduced here to define categories for siphuncles of very narrow and medium diameters respectively.

Siphuncle position. The position of the siphuncle within the confines of the chamber is generally described as being dorsal, ventral, central, subcentral, etc. Based on a large body of data, SOBOLEV (1989) has been able to develop an index for describing the position of the siphuncle for nautilids which can be extended to all other nautiloids. The index is calculated as Hc/Hw where Hc is the distance from the center of the siphuncle to the dorsum and Hw is the inner height of the whorl. The indices are categorized as: dorsal (> 0.0 to 0.14); subdorsal (> 0.14) to 0.26); dorso-central (> 0.26 to 0.37); centro-dorsal (> 0.37 to 0.45); central (> 0.45 to 0.55).

Length of connecting ring. This index quantifies the general length of the connecting ring by expressing the relationship between the maximum diameter of the connecting ring (Dr) and its length (Lr) as Dr/Lr. The categories are: long (> 0.0 to 0.43); average (> 0.43 to 0.70); short (> 0.70 to 1.0).

Connecting ring morphology. A straight-forward index for categorizing the morphology of the connecting rings using the maximum diameter of the connecting ring (Dr) and the diameter of the septal foramen (Ds) to produce Dr/Ds. The categories are: cylindrical (1.0 to 1.35); subcylindrical (> 1.35 to 1.80); nummuloidal (> 1.80 to 2.20).

Stratigraphic and geographic range of family

As now described, the family Liroceratidae consists of fourteen genera (Text-fig. 1), five of which occur in Triassic strata with proven ranges: *Paranautilus,* MOJSISOVICS 1902, *Tomponautilus* SOBOLEV 1989, *Indonautilus* MOJSISOVICS 1902, *Sibyllonautilus* DIENER 1915, and *Perunautilus* n. gen. The Permian occurrence of *Paranautilus* is not proven due to the questionable taxonomic position of *P. peregrinus* (WAAGEN) 1879 and *P. mokouensis* (YIN) 1933. *Tomponautilus* provides the earliest proven occurrence (Early Scythian) and there are no proven records of Late Scythian nautilids (Text-fig. 1). The geographic regions of occurrence of the Triassic liroceratids are indicated parenthetically in Text-fig. 1).

Systematics

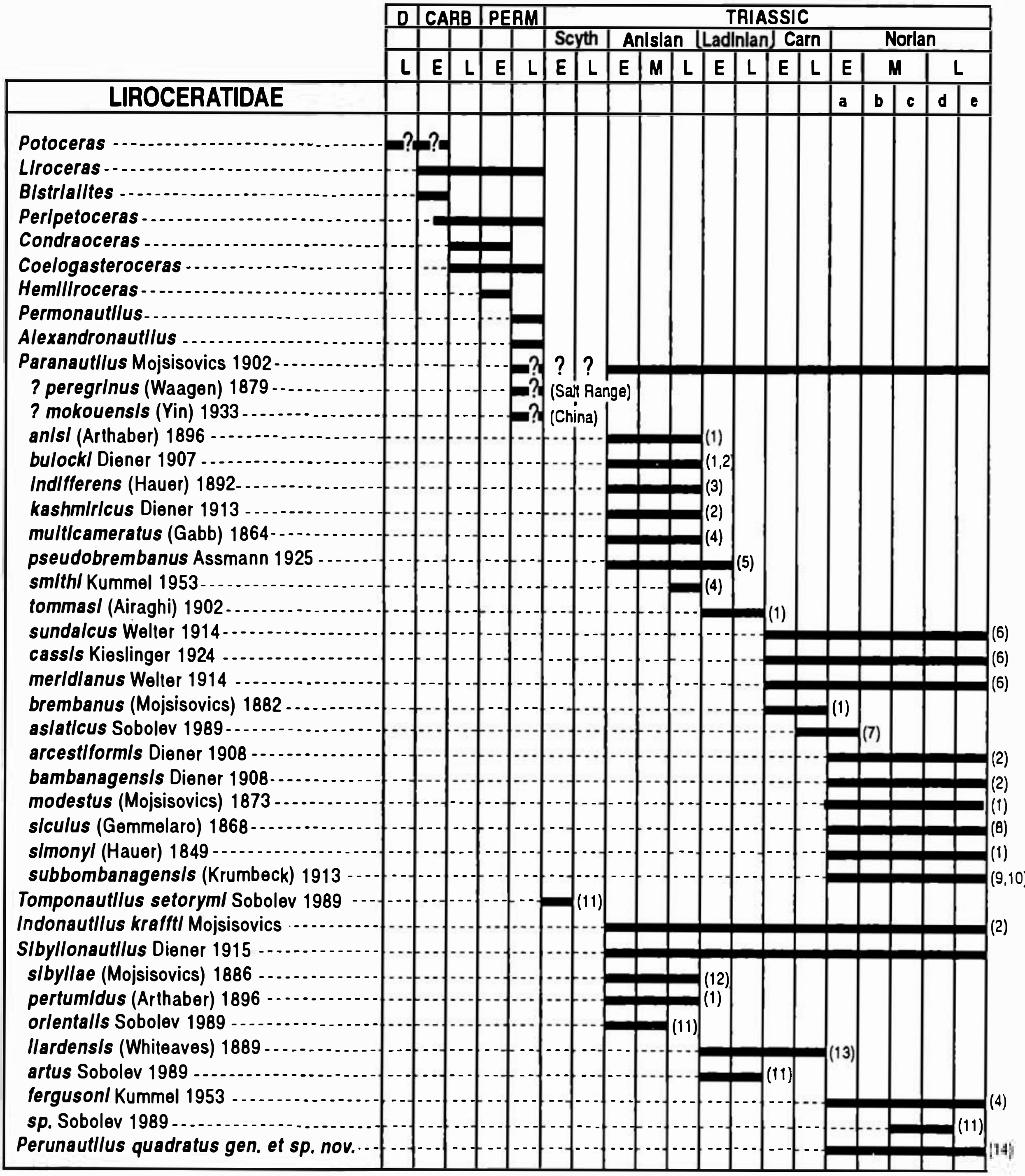
Class Cephalopoda

Superorder Nautiloidea

Order Nautilida

Suborder Liroceratina

Superfamily Lirocerataceae MILLER & YOUNGQUIST 1949



Text-fig. 1. Stratigraphic and geographic distribution of Liroceratidae (Cephalopoda, Nautilida). Stratigraphic information is given for all members of Liroceratidae with geographic information listed for Triassic species including two questionable Permian species of *Paranautilus*. Geographic regions are: 1, Alps; 2, Himalayas; 3, Yugoslavia; 4, Nevada; 5, Germany; 6, Timor; 7, Omolon Massif along upper reaches of Omolon River, northeast Siberia; 8, Sicily; 9, Indonesia; 10, Iran; 11, Taymyr Peninsula and lower reaches of Olenek River, northern Siberia; 12, Spitzbergen; 13, British Columbia; 14, Peru. Norian zones are those recognized in north and northeastern Siberia (SOBOLEV 1989): a, *Pterosirenites obrucevi*; b, *Otapiria ussuriensis*; c, *Monotis scutiformis*; d, *Monotis ochotica*; e, *Tosapecten efimovae*.

Family Liroceratidae MILLER & YOUNGQUIST 1949

Genus *Perunautilus* CRICK & SOBOLEV n. gen.

Name: From geographic association with Peru.

Type species: *Perunautilus quadratus* sp. nov.; Norian.

Diagnosis: Involute, thickly discoidal conch, with rapidly expanding whorls and tendency to be depressed in dorsal-ventral plane. Whorl section wide, roundly trapezoidal. Ventral side broad, slightly prominent. Umbilical and ventral shoulders broadly rounded, conspicuous. Surface of couch is smooth. Suture line slightly sinuous, with broad and shallow ventral and lateral lobes. Shallow annular lobe present on the dorsum. Siphuncle narrow, near to subdorsal. Septal necks suborthochoanitic. Connecting rings usually short, thin, subcylindrical with rounded outlines.

Species included: Type species.

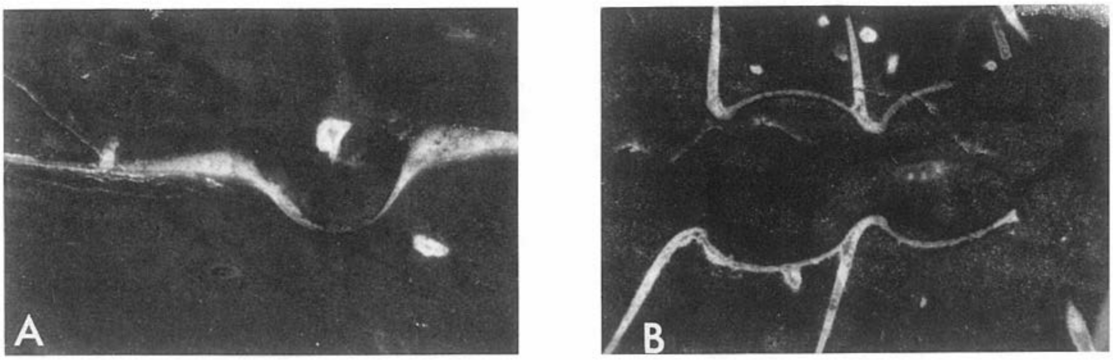
Remarks and comparisons: We consider the new genus to be a member of the family Liroceratidae MILLER & YOUNGQUIST 1949 on the basis of such characteristic morphological features as being involute, without ornamentation, conch with rounded, rapidly expanding whorls and a slightly sinuous suture line. At the same time *Perunautilus* has rather unusual features. It differs from the most similar form, *Tomponautilus* SOBOLEV, 1989, in shape of the conch and by the structure of the siphuncle. The two genera are notable in that they both share the feature of an annular lobe in the suture line (Plate 1, Fig. 4). *Tomponautilus* SOBOLEV, 1989 consisting of one species, *T. setoryni* SOBOLEV (1989, p. 90, pl. 32, fig. 1–3, pl. 33, fig. 1, text-figs. 50 & 51), was described from the lower Triassic *Otoceras* beds of Siberia. *Tomponautilus* has a wide siphuncle with loxochoanitic septal necks and thick connecting rings of nummuloidal shape. The connecting rings are attached at oral ends to outside surfaces of frontal septal necks by a right angle, covering them fully. The siphuncle of *Perunautilus* is narrow, the septal necks are suborthochoanitic, the connecting rings are thin, subcylindrical with rounded outlines. The connecting rings of *Perunautilus* are attached to septal necks by rather sharp angles and cover only their smaller part. *Perunautilus* differs from the genus *Paranautilus* MOJSISOVICS, 1902, the typical representatives of which are *P. simonyi* (HAUER) (MOJSISOVICS, 1902, p. 207, pl. 1, fig. 2) and *P. modestus* MOJSISOVICS) (1873–1875, p. 29, pl. 15, fig. 2) by possessing a wide, thickly discoidal conch depressed in dorso-ventral plane, with rounded, but distinct ventral and umbilical shoulders, a maximum width of whorls just outside umbilical shoulders, and a suture line with a ventral lobe and a dorsal annular lobe. The conch of *Paranautilus* is higher than wide, laterally compressed, with a slightly differentiated surface, without distinct ventral and umbilical shoulders and with maximal width of whorls usually in the middle of lateral sides. The suture line of *Paranautilus* usually exhibits a distinct ventral saddle but it may be straight. *Perunautilus* differs from the genus *Indonautilus* MOJSISOVICS, 1902 by being depressed in dorsal-ventral plane, its thickly discoidal conch, and having a broad ventral side. The conch of *Indonautilus* is usually compressed on lateral sides, rather higher than wide with distinctly differentiated narrow and flat ventral sides which are separated from lateral sides by angular shoulders. The only other nautilid genus to which *Perunautilus* shares a similarity is *Sibyllonautilus* DIENER 1915 and the similarity is that of rapid expansion of the conch. *Sibyllonautilus* exhibits a more evolute conch with a well differentiated surface in the umbilicus region (angular umbilical shoulders and flattened umbilical walls) and a more highly differentiated suture line characterized by the presence of a distinct annular lobe.

A poorly preserved specimen of *Paranautilus* from the Upper Triassic of Nevada described by KUMMEL (1953, p. 72, pl. 8, fig. 8, 9) may belong to *Perunautilus.* The occurrence and age of this specimen were better defined by SILBERLING (1959, p. 321) who reported that the specimen came from the lower Norian Mojsisovicsites kerri zone of the calcareous shale member of Luning Formation, Soshone Mountains, Nevada. This specimen is an immature individual consisting of a half first and a half second whorls, characterized by involute, thickly discoidal conch with slightly sinuous suture line, and exhibits rather inconspicuous ventral and lateral lobes. The preservational state of the specimen and that it represents an immature stage of growth prevent a definitive analysis of its generic affinities.

Occurrence: Norian stage, central Peru, ? Nevada, U.S.A.

Perunautilus quadratus CRICK & SOBOLEV n. sp.

Plate 1, Figs. 1–3, Text-fig. 2



Text-fig. 2. A. Annular lobe (UMIP 12311). 4× . – B. Suborthochoanitic septal neck and subcylindrical connecting ring geometry (IMIP 12312). 3.75× .

Name: Latin for the distinctive four-cornered appearance of the mature conch in transverse section.

Holotype: UMIP 12311, University of Montana, Missoula, the most complete specimen; Upper Triassic, Norian stage, Chambara Formation at Shalipayco where specimens occur in the lower portion of the section. See contribution of STANLEY for details of sections and localities.

Description: Conch very large, involute, thickly discoidal, depressed in dorsal-ventral plane in late whorls. First whorl closely coiled, very large. Cross section of the conch in early whorls rounded, in later whorls roundly trapezoidal with whorl width greater than height. The maximum width is just outside umbilical shoulders. In later whorls ventral side is broad, slightly rounded, lateral sides are slightly convex. Umbilical and ventral shoulders are widely rounded and conspicuous. Umbilical walls are slightly convex, abrupt. Whorls are nearly complete covering the previous ones. Chambers of the phragmocone are short, umbilicus narrow, deep.

Conch surface is smooth. Septa closely spaced. Suture line in late whorls is slightly sinuous, with conspicuous broad and shallow ventral and lateral lobes and a shallow dorsal annular lobe (Text-fig. 2A). Siphuncle stenosiphonate (Ds/Hw, 0.089), and remains subdorsal throughout ontogeny (Hc/Hw, 0.178). Septal necks suborthochoanitic (Text-fig. 2B). Connecting rings thin, short (Dr/Lr, 0.83), cylindrical (Dr/Dn, 1.25) with rounded outlines. Connecting rings attached to front of septal neck surfaces by the ends at sharp angles and cover only a small apical part of preceding septum.

Measurements (mm) and ratios for the holotype (UMIP 12312) and paratypes (UMIP 12311 & 12313).

Specimen	W	H	W/H	Ds	Hw	Ds/Hw	Hc	Hc/Hw	Dr	Dr/Dn	Lr	Dr/Lr
12311	78	59	1.32	4.0	45	0.089	8.0	0.178	5.0	1.25	6.0	0.83
12312	83	62	1.34	4.5	49	0.092	9.0	0.184	6.0	1.33	6.3	0.95
12313	60	45	1.33	3.3	37	0.089	6.7	0.181	4.2	1.27	5.0	0.84

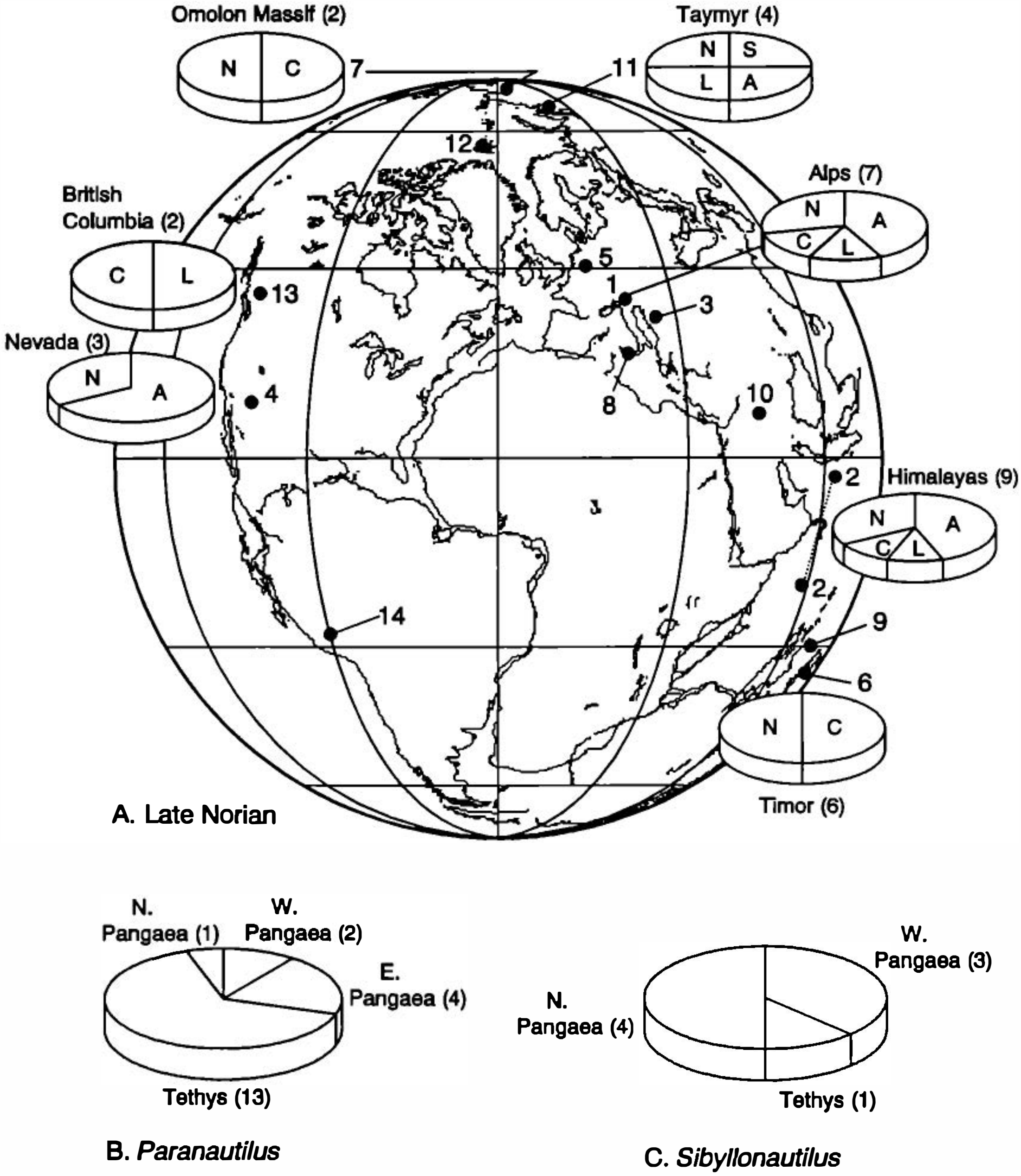
All measurements for an individual were taken at the same location on the shell. Abbreviations as follows: W, whorl width; H, whorl height; Ds, diameter of siphuncle foramen; Hw, inner height of whorl from umbilicus to venter; Hc, distance from center of siphuncle to dorsum; Dr, maximum diameter of connecting ring; Lr, length of connecting ring. Ratios are used to normalize the effects of size.

Occurrence: Upper Triassic, Norian stage, Peru.

Material: Central Peru at locality Shalypayco (85-SH-7). Three specimens: UMIP No. 12311, 12312, 12313.

Biogeographic implications of liroceratid distributions

Text-fig. 3 illustrates the distribution of Triassic species of Liroceratidae in the context of Late Norian paleogeography. Although not all species are inclusive of the Norian (Text-fig. 1), the relative change in positions of most landmasses from Anisian through Norian is small enough to allow the Norian to serve as a base from which to illustrate the geographic position of all species. Text-fig. 3A illustrates the pandemic nature of Triassic liroceratids as they existed around the margin of Pangaea and within the region of Tethys. Pie charts for localities



Text-fig. 3. Distribution of Triassic members of Liroceratidae at latest Norian, 210 MY. A. Occurrences of Triassic species of Liroceratidae are plotted on Late Norian paleogeography (210 MY). Numbered dots are localities identified in the caption to Text-fig. 1. The questionable position of locality 2 (Himalayas) reflects uncertainty about which plate originally contained the locality. Pie charts for localities with more than one occurrence show relative diversity for Triassic ages: A, Anisian; L, Ladinian; C, Carnian; N, Norian. Number of occurrences shown parenthentically after locality name. Actual species composition of localities can also be determined from comparison with Text-fig. 1. Reconstruction generated with PALEOMAP-PC by DAVID WALSH, Paleomap Project, University of Texas at Arlington. B. Diversity of *Paranautilus* species within four regions. C. Diversity of *Sibyllonautilus* species within three regions.

with more than one occurrence of liroceratid show the number of species during any one Triassic age for a given region. The distribution of nautilids at high northern latitudes is uncommon for nautilids in general, including extant *Nautilus* which is generally confined to 35 degrees N & S latitude. Assuming that liroceratids maintained the same intolerance of high latitude water temperatures, their presence and persistence at high latitudes is another indication of generally warm conditions at these latitudes. While this is presumably the case, it is interesting to detail the distribution of the two genera responsible for 90 % of Triassic liroceratid species, *Paranautilus* and *Sibyllonautilus.* The distributions of species belonging to these genera by four general regions are shown in Text-figure 3B and 3C and document that species of *Paranautilus* are far more common in the region of the Tethys while species of *Sibyllonautilus* are more common in northern and western margins of Pangaea and do not occur along the eastern margin of Pangaea (localities 4, 13, 14). Though neither distribution is exclusionary between Tethys and northern Pangaea, *Paranautilus* and *Sibyllonautilus* are each represented by only one species of in regions of northern Pangaea and Tethys respectively, the distribution of *Paranautilus* can be described as low latitude and that of *Sibyllonautilus* as high latitude.

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Explanation of the plate

Plate 1

Fig. 1. *Perunautilus quadratus* Crick & Sobolev. Holotype (UMIP 12312) Ventral view of youngest portion of phragmocone just posterior of the living chamber. From Shalypayco (85-SH-7). 0.65 ×.

Fig. 2. *Perunautilus quadratus* Crick & Sobolev. Paratype (UMIP 12311). View of youngest septum (rear of living chamber) showing the square or rectangular nature of the cross-section. From Shalypayco (85-SH-7). 0.5 ×.

Fig. 3. *Perunautilus quadratus* Crick & Sobolev. Paratype (UMIP 12313). Flank view of a near complete specimen although erosion has removed a portion of the phragmocone and living chamber. From Shalypayco (85-SH-7). 0.65 ×.

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2

3

R. E. Crick and E. S. Sobolev: *Perunautilus quadratus* n. gen. et sp.