

Cephalopods of the San José Formation of Peru (Floian, Early Ordovician) and their paleogeographic significance

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Non-technical Summary.—Fossil remains of extinct relatives of cephalopods are known to occur in Peruvian strata of Ordovician age (~485–444 million years old) for a long time. However, they remain poorly known today. Here, we describe for the first time specimens that were collected from strata of the San José Formation of the Kimbiri and Inambari areas, southeastern Peru. The assemblage contains five species; one of them, *Bactroceras cocafolium*, is new to science. One other species is known from strata of the same age from elsewhere in the central Andes. The five species also show a relationship with cephalopod assemblages known from the old continents Gondwana and Avalonia.

Abstract.—The existence of Ordovician Peruvian cephalopods has been known since at least the 1910s. However, they have not been effectively documented previously with only a few described taxa listed in open nomenclature. Here, we describe a cephalopod assemblage at the finest taxonomic level possible. The specimens were collected from the Floian section (*Baltograptus minutus* graptolite Zone) of the San José Formation from the Kimbiri area, northwest of Cuzco (= Cusco), and from a section along the Inambari River, southeastern Peru. The dark mudstone-siltstone of the San José Formation was deposited within the Central Andean Basin. The assemblage contains five species of small orthoceracones belonging to four families and three orders, consisting of one indeterminate dissidocerid, one bathmocerotid (*Saloceras* sp.), one rioceratid (*Rioceras?* sp.), and two baltoceratids belonging to *Annbactroceras greccostatum* (Kobayashi, 1937), and *Bactroceras cocafolium* new species. The dominance of small orthoceracones is typical for early Paleozoic pelagic cephalopod assemblages. One species, *A. greccostatum*, is known from elsewhere in the Central Andean Basin. The other taxa indicate a peri-Gondwana-Avalonia paleogeographical relationship of the cephalopod fauna, which is consistent with previously published data from brachiopods and trilobites.

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Introduction

Ordovician cephalopods of Peru are poorly known, although they are not rare and were first mentioned by Lissón (1911, p. 146). This early work lists a single orthoceracone cephalopod in the Ordovician strata of the Ambo-Huánuco region of the Eastern Cordillera in Central Peru (see also Lissón and Boit, 1924, p. 121), a place well known for its abundant Darriwilian graptolites (see e.g., Maletz et al., 2010).

Bulman (1931, p. 99) identified a questionable endocerid cephalopod from Sandbian graptolitic shales of the Huichiyuni locality, south of San Juan del Oro, Eastern Cordillera (Fig. 1.1, loc. E). Douglas (1933, p. 340, 341, pl. 29, figs. 1, 2) reported endocerid and orthocerid occurrences in

Darriwilian graptolitic shales from west of Quincemil, Eastern Cordillera (Fig. 1.1, loc. B), and Laubacher (1974, p. 33, 35) mentioned cephalopods from presumed Darriwilian strata at the Inambari River section at Carcelpuncco (Fig. 1.1, loc. C). All of these records of cephalopods are from the San José Formation (late Tremadocian–early Sandbian) of central and southeastern Peru.

Orthoceracone cephalopod occurrences are also known from Darriwilian graptolitic shales of the Contaya Formation of the Contaya Arch in the Amazonian plains of northeastern Peru, close to the Brazilian border (Newell and Tafur, 1943, p. 8; 1944, p. 541; Hughes et al., 1980, p. 15). Furthermore, Laubacher (1974, p. 36) recorded cephalopod occurrences in the Sandia Formation (Late Ordovician), in the La Pampa River valley, north of the Santo Domingo mining camp (Fig. 1.1, loc. D) yielding also ‘Caradocian’ trilobites and brachiopods. *Pachendoceras* sp. indet. was recorded by Romero et al. (1995, p. 13)

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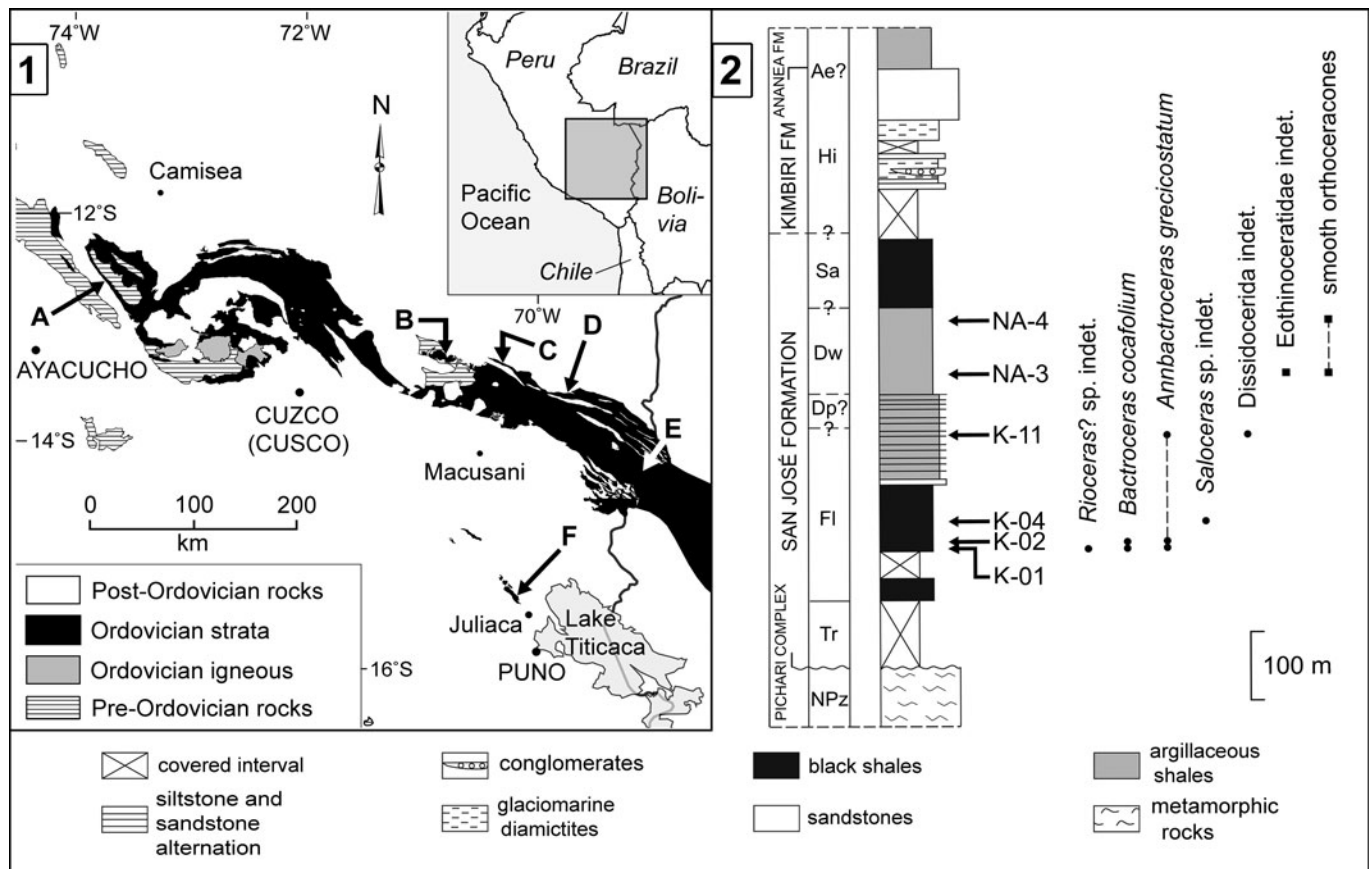


Figure 1. (1) Geological overview of SE Peru (inset map), showing the extent of the Ordovician sedimentary rocks and the location of some of the Ordovician localities with cephalopods cited in the text: A, Apurímac River valley (Kimbiri Alto, Libertad and Nueva Alianza sections, see detailed map in Fig. 2); B, Yanarco River west of Quincemil; C, Carcelpunco canyon, Inambari River; D, La Pampa River north of Santo Domingo; E, Yanahuaya area south of San Juan del Oro; F, Calapuja area. (2) Simplified stratigraphic section from Kimbiri (= Kashiroveni; Fig. 2, loc. 3), with vertical distribution of Floian taxa identified from four horizons. Data from Darriwilian cephalopods (black squares) come from the nearby Nueva Alianza locality, NW of Kimbiri (Fig. 2, loc. 2). Ae, Aeronian; Dp, Dapingian; Dw, Darriwilian; Fl, Floian; Fm, Formation; Gp, Group; Hi, Hirnantian; NPz, Neoproterozoic; Ord, Ordovician; Sa, Sandbian; Tr, Tremadocian.

in Late Ordovician strata from the Calapuja Formation at the Hacienda Buena Vista fossil locality (Fig. 1.1, loc. F) within the Peruvian Altiplano west of Lake Titicaca. A small suite of cephalopods was collected by one of the authors (JCG-M) from Sandbian strata of the Calapuja Formation of the Peruvian Altiplano, west of Lake Titicaca, and awaits taxonomic description in a future paper.

The Peruvian Geological Survey/INGEMMET mapping program led to the discovery of new localities with cephalopods in the San José Formation of the Eastern Cordillera. De la Cruz and Carpio Ronquillo (1996, p. 140) mentioned the occurrence of *Endoceras* sp. indet. and *Protocycloceras* cf. *P. smithvillense* Ulrich et al., 1944 in two ‘Llanvirnian’ localities south of Yanahuaya, to the south of San Juan del Oro (Fig. 1.1, loc. E). In the Apurímac River valley northwest of Ayacucho (Fig. 1.1, loc. A; Fig. 2, loc. 4), Valencia Muñoz et al. (2021, p. 32) found a flattened external mold of a body chamber of an orthoceracone cephalopod, wrongly identified as *Conularia* sp. indet. From a neighboring locality (Fig. 2, loc. 5), Latorre Borda et al. (2021, fig. 2.16a) illustrated a flattened body chamber in connection with the siphuncle, identified as “Endoceratida ind.,” which was obtained from a probable Darriwilian assemblage of graptolites, brachiopods, and trilobites.

The Darriwilian cephalopods of the San José Formation described by Douglas (1933) were reviewed by Evans (2007). However, the poor and fragmentary preservation of the specimens allowed only relatively general determinations in open nomenclature. The revision showed that the assemblage is dominated by small orthoceracones, which were interpreted as representing open-water habitats with far-ranging paleogeographic affinities spanning from Western Gondwana to Avalonia and Armorica (Evans, 2007).

Here, we describe an assemblage of relatively well-preserved cephalopods from the Floian part of the San José Formation. This allows for a comparison with coeval Eastern Cordilleran assemblages from Bolivia and Argentina and more generally contributes toward a better understanding of the cephalopod evolution during the Floian Stage, which is a critical interval for cephalopod evolution (Pohle et al., 2022).

Geological setting

The material described herein was collected from the San José Formation, which is exposed in roughly northwest/southeast-oriented sedimentary belts associated with the Cordillera Oriental in southeastern Peru and Bolivia. The Cordillera Oriental continues southward into northwestern Argentina. During the

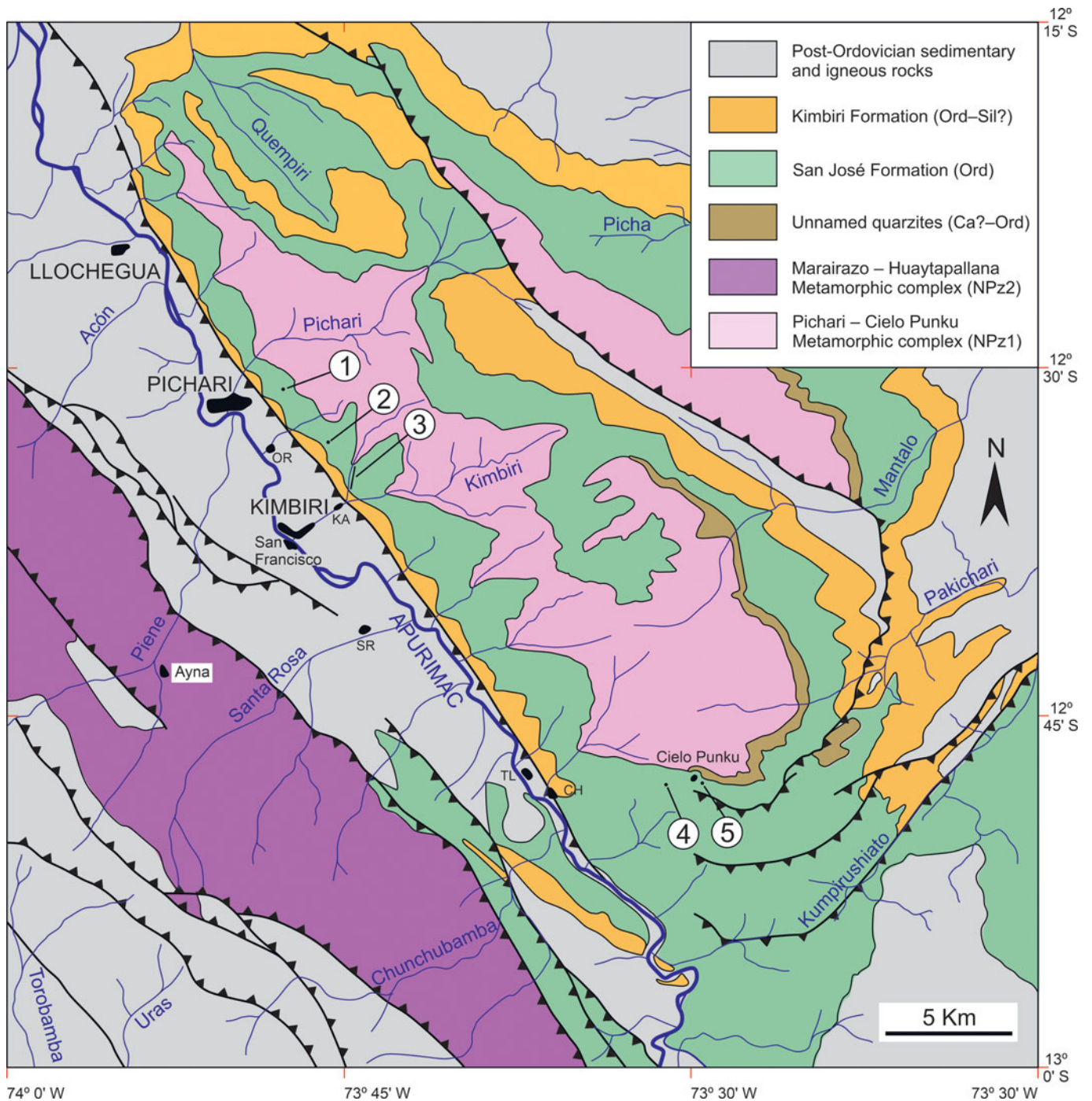


Figure 2. Geological sketch map of the fossil localities in the Apurímac River valley bearing Ordovician cephalopods. 1, Libertad (LIB); 2, Nueva Alianza (NA-3 and NA-4); 3, Kimbiri (Kashiroveni stream) section (K-01 to K-11); 4, Cielo Punku 1 (fossil sample GR52A-19-53 of Valencia Muñoz et al., 2021); 5, Cielo Punku 2 (fossil sample GR53A-19-10 of Latorre Borda et al., 2021). Base map modified by JCG-M after Gómez Cahuya et al. (2021), Valencia Muñoz et al. (2021), and Latorre Borda et al. (2021). CH, Chirumpiari; KA, Kimbiri Alto; OR, Oroya; SR, Santa Rosa; TL, Tahuantisyuyo Lobo. The Cambrian?–Early Ordovician ‘unnamed quartzite’ unit was correlated to the Ollantaytambo Formation in previous geological maps (Latorre Borda et al., 2021; Valencia Muñoz et al., 2021), but later has been reassigned to the Pennsylvanian (late Carboniferous) in its type area north of Cuzco (Hodgin et al., 2021).

Cambrian–Ordovician, these strata formed part of the Central Andean Basin (Astini, 2003).

This feature formed as a vast retroarc foreland basin along the accretionary Proto-Andean margin of South America. During the Ordovician, its tectonic framework was strongly dynamic with regionally and temporally contrasting depositional rates and directions (see review by De la Puente

and Astini, 2023). Therefore, the Ordovician deposits of the Central Andean Basin are divided into several stratigraphical units depending on the country, paleogeography, and geotectonic position (see e.g., Benedetto et al., 2009; Waisfeld et al., 2023).

The material described herein was collected from several outcrops of the San José Formation along the northeastern

bank of the Apurímac River, between Pichari and Kimbiri (Fig. 2), and in a single fluvial section located in the Pongo (= canyon) of Carcelpuncco on the Inambari River, southeast of Cuesta Blanca (Fig. 1.1, loc. B). Ordovician fossiliferous localities in the first area (Fig. 1.1, loc. A) were discovered during the mapping of the Llochegua and San Francisco/Ayna quadrangles (Monge et al., 1998). The Inambari River section (Fig. 1.1, loc. B) has been known since the 1970s (Dávila and Ponce de León, 1971; Laubacher, 1974; see also Palacios et al., 1996).

Most of the studied specimens come from a single section located north of the village of Kimbiri Alto, along the trail parallel to the Kashiroveni Stream above its confluence with the Kimbiri River—one of the tributaries on the right bank of the Apurímac River, ~80 km northeast of the city of Ayacucho (Figs. 1.2; 2, loc. 3). The dominantly shaly San José Formation is up to 700 m thick and lies unconformably upon the metamorphic Pichari-Cielo Punku Complex (Neoproterozoic). Its lower (but not basal) part has yielded Tremadocian to earliest Floian graptolites (Gutiérrez-Marco et al., 2019a). These strata are overlain by beds partially rich in shelly fauna, documenting Floian to lower Sandbian strata toward the middle and upper part of the formation (see references below).

The Kimbiri section (= ‘Quimbiri’ in older spelling) was exposed in 2006 along a new trail built by a gas exploration company that operates in the Camisea Field. Its eastern slope exposed a few hundred meters of Ordovician fossiliferous strata belonging to the San José Formation that were carefully sampled in 2006, 2016, and 2018, before small landslides, local erosion, and the tropical jungle climate concealed parts of the section.

This material has resulted in several paleontological descriptions of the faunal record of the Kimbiri section: Lower Ordovician conodonts (Carlorosi et al., 2014); trilobites (Gutiérrez-Marco et al., 2015; Fortey and Gutiérrez-Marco, 2022); lightly sclerotized arthropods (Gutiérrez-Marco et al., 2019b); graptolites (Gutiérrez-Marco et al., 2019a); and ostracods (Gutiérrez-Marco et al., 2019c).

The cephalopods, reported herein, come from fossiliferous beds K-01, K-02, and K-04, ~170–190 m above the base of the San José Formation, within an interval yielding graptolites of the late Floian *Baltograptus minutus* Biozone (Gutiérrez-Marco et al., 2019a). The same age is extended tentatively to the upper K-11 cephalopod horizon, which has so far yielded few graptolites (*Pseudophyllograptus* Cooper and Fortey, 1982, *Baltograptus?* Maletz, 1994), occurring in sand-dominated strata ~140 m above the K-04 horizon. The late Floian age indicated by the graptolites also agrees with the scarce conodont record indicative of the upper part of the *Oepikodus evae* Biozone, identified by Carolosi et al. (2014) in the K-02 horizon from the carbonate infilling of a single internal mold of the body chamber of an ‘endoceratid’ preserved in black shales.

Additional material from along the Apurímac River was collected from two localities northwest of the Kimbiri section: Libertad (LIB; Fig. 2, loc. 1), situated along the mountain trail between this town and the city of Pichari, which can be approximately correlated with the black shales placed slightly above the K-04 fossiliferous horizon, yielding graptolites of the *B. minutus* Zone (Gutiérrez-Marco et al., 2019a). The second is the Nueva Alianza section (NA; Fig. 2, loc. 2), located along the mountain trail between this small village and Oroya. The upper part of the

section (paleontological horizons NA-3, NA-4) consists of highly fossiliferous (brachiopods and trilobites) argillaceous shales, which weather to reddish colors. This part of the section yielded some middle Darriwilian cephalopods that complement the data of the Kimbiri section (Fig. 1.2). The strata from the main fossil site near Nueva Alianza are roughly coeval with the Yanaorco River locality, located 300 km further east (Fig. 1.1, loc. B), from where Douglas (1933) and Evans (2007) reported the only previously published descriptions of Peruvian Ordovician cephalopods.

The locality of Douglas’ (1933) collection west of Quince-mil is briefly reviewed herein, because of discrepancies with Evans’ (2007, fig. 1) description: Douglas (1933, fig. 1) indicated a point located on the right bank of the Yanaorco River (ex ‘Yanahurco’), upstream of its eastern confluence with the Quebrada Collpamayo (ex ‘Yuscamayo’). According to current geological maps (Palacios et al., 1996), the latter runs almost entirely through Quaternary sediments, whereas the lower Yanaorco valley would be the most probable place for Douglas’ (1933) locality because it traverses a large outcrop of shales attributed to the San José Formation (erroneously attributed to the Devonian Cabanillas Group; León and Chumpitaz, 2021). In Evans (2007, fig. 1) account, the Douglas’ (1933) locality is placed less precisely, in an area spanning the left bank of the lower Yanaorco valley toward the Quebrada Collpamayo.

Finally, a single cephalopod, collected from the section in the Carcelpuncco canyon of the Inambari River (Fig. 1.1, loc. C), comes from the lower part of the San José Formation. It was recovered from the horizon CB-87 that is derived from Gutiérrez-Marco and Villas’ (2007) brachiopod horizon ‘D.’ This fossiliferous horizon lies ~20 m above a thin limestone bed that contains conodonts from the upper part of the *Oepikodus evae* Zone of Floian age (Gutiérrez-Marco et al., 2008). The position of locality CB-87 was marked as point ‘D’ by Gutiérrez-Marco and Villas (2007, figs. 1, 2).

Materials

The available material consists of recrystallized shells, steinkerns, and impressions preserved within limonite-rich, black lime-mudstone nodules and black shales. The shell material is preserved as recrystallized black calcite. The cross sections of the specimens are slightly diagenetically compressed to strongly flattened when preserved in the shales. The specimens within the nodules are in most cases only slightly diagenetically deformed. Imprints of bryozoan epizoans occur on the conch surface of one specimen (CPI-10097; Fig. 5.5).

Repository and institutional abbreviation.—The material described herein is deposited in the paleontological collection of the Peruvian Geological Survey (INGEMMET) in Lima under the accession numbers CPI-10075 to CPI-10097.

Systematic paleontology

Order Dissidocerida Zhuravleva, 1994
Dissidocerida indet.
Figures 3.14, 4.1, 4.2



Figure 3. Cephalopods from the Kimbiri section, Apurimac River valley, Peru, Floian Stage, Ordovician: (1, 2) *Saloceras* sp. indet., CPI-10077, K-04 horizon: (1) ventral view; (2) dorsal view. (3–6, 8, 13) *Annbactroceras grecicostatium* (Kobayashi, 1937): (3, 4) CPI-10083, horizon K-02: (3) ventral view, note deep V-shaped, healed bite mark; (4) lateral view with venter toward right side; (5) CPI-10082, horizon K-02, adoral view; (6) CPI-10084, horizon K-02, ventral view; (8) CPI-10087, horizon K-11, lateral view; (13) CPI-10079, neotype, horizon K-01, lateral view. (7) *Rioceras?* sp. indet., CPI-10078, horizon K-01, ventral view. (9, 10, 12) *Bactroceras cocafoium* n. sp., holotype, CPI-10092, horizon K-02: (9) lateral view, venter toward right side; (10) adoral view; (12) CPI-10093a, horizon K-02, ventral view of apical portion (note the partly broken apex). (11) *Saloceras* sp. indet., CPI-10076, horizon K-04, lateral view. (14) Dissidocera indet., CPI-10075, horizon K-11. Scale bars = 5 mm, same scale bar for specimens (1–5, 7, 8, 11, 13), for specimen (9, 10), respectively. Specimens (1–12) whitened with ammonium chloride.

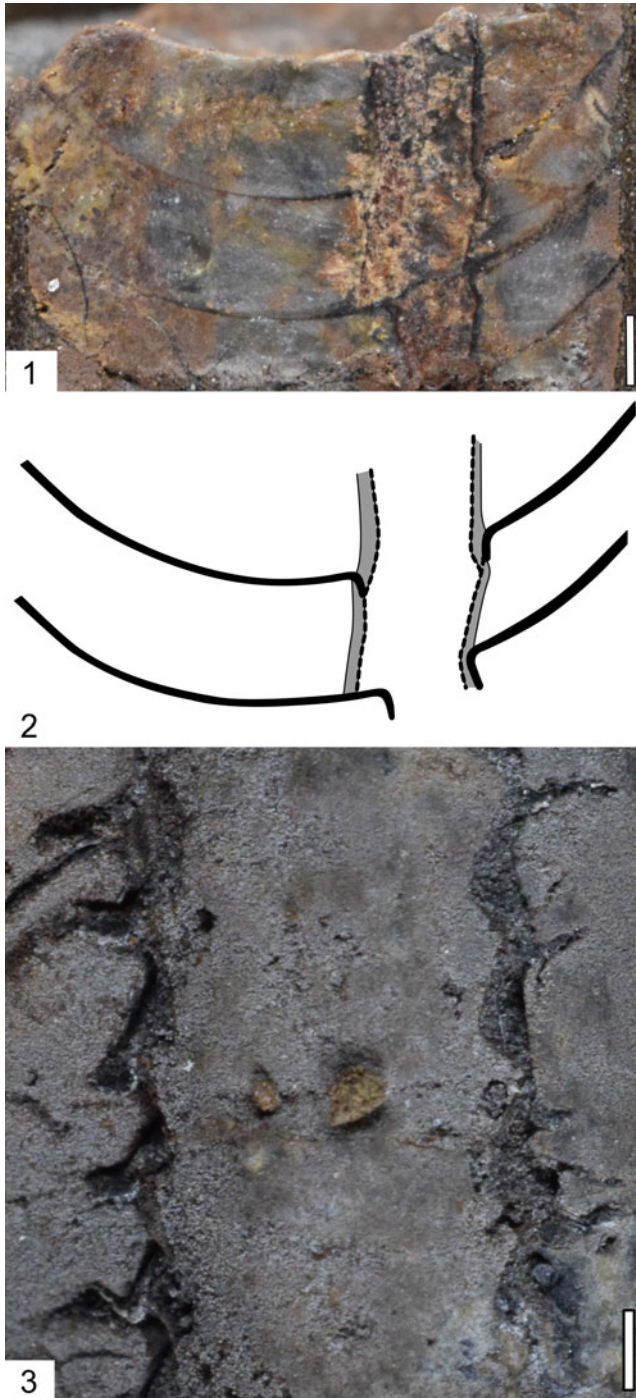


Figure 4. Details of the siphuncle of cephalopods from the Kimbiri section, Apurimac River valley, Peru, Floian Stage, Ordovician: (1) Dissidocerida indet., CPI-10075, horizon K-11, median section (same as Fig. 3.14); (2) interpretative drawing of (1). black = septa; gray = connecting ring; dashed line = inner surface of connecting ring. (3) *Saloceras* sp. indet., CPI-10077, horizon K-04 (same as Fig. 3.1, 3.2). Scale bar = 1 mm.

Description.—The specimen consists of three fragments of a phragmocone embedded in sediment matrix. Details of the conch surface are not preserved. However, it was not or only very weakly annulated. The straight conch has a circular cross section and expands from 6–8.5 mm along a distance of 23 mm (angle of expansion $\sim 6^\circ$). The largest diameter of the fragment

is 10 mm. At a conch diameter of 8.3 mm, the septal distance is 1.6 mm (0.19 of corresponding conch cross section), the siphuncular diameter is 1.8 mm (0.22 of corresponding conch cross section), and the siphuncle is positioned 2 mm from conch margin (0.24 of corresponding conch cross section). The septal necks are orthochoanitic. The connecting rings are partly distorted and were originally either slightly concave or convex or concavoconvex. Parietal deposits occur at siphuncular margins directed toward the conch margin and toward the conch center.

Material.—CPI-10075, Kimbiri section bed K-11, *Baltograptus minutus* graptolite Zone, Floian, Ordovician.

Remarks.—The poor and fragmentary preservation of this single specimen does not allow for the erection of a taxon although it does not belong to any known genus and species. The specimen is most similar to a yet unnamed group of orthocones with parietal endosiphuncular deposits, which include: *Destombesiceras zagorensis* (Kröger and Lefebvre, 2012) from the Upper Fezouata Formation, Morocco (early to mid-Floian) and *Glenisteroceras obscurum* Flower in Flower and Teichert, 1957 from the Fort Cassin Formation, New York, USA (early Floian). The latter two genera have been previously classified within the Apocronoceratidae Flower in Flower and Teichert, 1957 within the Discosorida (see e.g., Kröger and Lefebvre, 2012). *Glenisteroceras* Flower in Flower and Teichert, 1957 differs mostly in having cyrtchoanitic septal necks, and in *Destombesiceras* Kröger and Lefebvre, 2012 the siphuncle is positioned closer to the conch margin.

The family Apocronoceratidae is poorly supported by Bayesian phylogenetic inference (Pohle et al., 2022) and there is a high probability that it is paraphyletic. Moreover, the group of *Destombesiceras* + *Glenisteroceras* is a sister group to the clade containing actinocerids, orthocerids, and pseudorthocerids within the Dissidocerida (Pohle et al., 2022). Therefore, the Kimbiri specimen described herein is classified within the Dissidocerida. The poorly preserved specimen gives additional evidence for the presence of a characteristic group of Floian orthocones with parietal deposits.

Order Cyrtocerinida Flower, 1964
Family Bathmoceratidae Gill, 1871
Genus *Saloceras* Evans, 2005

Type species.—*Orthoceras sericeum* Salter in Ramsay, 1866, from the Tremadocian of North Wales, UK; by original designation.

Diagnosis.—Orthoconic bathmoceratids with circular to slightly depressed cross section and moderate angle of expansion; sutures straight and directly transverse with ventral saddle over siphuncle; siphuncle marginal, most forms with diameter 0.2–0.5 of corresponding phragmocone cross section, less frequently smaller; septal necks achoanitic to weakly orthochoanitic; siphuncular segments strongly concave with connecting rings asymmetrically thickened, protruding into the siphuncle; siphonal diaphragms present (diagnosis after Cichowolski et al., 2015).

Saloceras sp. indet.
 Figures 3.1, 3.2, 3.11, 4.3

Description.—Specimen CPI-10077 (Figs. 3.1, 3.2, 4.3) is a slightly diagenetically compressed straight fragment of a phragmocone. The conch surface is not preserved and the prosiphuncular part area is partly eroded, exposing parts of the siphuncle along the longitudinal axis. The specimen has a total length of 38 mm, and the conch widths of 14–15 mm are 15 mm apart (angle of expansion is 4°). The septal spacing is tight with eight chambers at a length similar to the corresponding conch cross section. A weak annulation is visible at the antisiphuncular side with a distance between the shallow annuli of ~5 mm (approximately three chambers per annulation). The siphuncle is ~4 mm in diameter at a conch width of 15 mm (relative siphuncular diameter ~0.3). Connecting rings are 0.5 mm thick and form concave segments.

Specimen CPI-10076 (Fig. 3.11) is a fragment of a body chamber and phragmocone. The phragmocone is eroded roughly along the dorsoventral axis exposing the siphuncle. It is heavily distorted and does not allow for measurements. However, the steinkerns of the siphuncle and the body chamber are well preserved. At the base of the body chamber the conch height is 22 mm. The preserved part of the body chamber has a length of 24 mm and a maximum conch height of 25 mm (angle of expansion ~8°). The depth of the septal curvature is ~4 mm at the base of the body chamber. The conch surface is poorly preserved, but apparently lacks annulation or ornamentation. The septal distance directly adapical of the body chamber equals seven or eight chambers per distance, similar to the corresponding conch height. The siphuncle is marginal with a diameter of 6 mm at the base of the body chamber (relative siphuncular diameter ~0.27) and the siphuncular segments are concave.

Materials.—CPI-10076 and CPI-10077, Kimbiri section bed K-04, *Baltograptus minutus* graptolite Zone, Floian, Ordovician.

Remarks.—The fragmentary preservation of the two specimens, the lack of diagnostic conch surface characters, and the diagenetically distorted conch cross section preclude any species level determination. The weak or absent annulation of the two specimens is similar to that of *Saloceras sikus* Cichowolski et al., 2015, known from the Acoite Formation, Floian Stage, Jujuy, Argentina. The two Peruvian specimens also fall within the range of variation of *S. sikus* with respect to chamber spacing and siphuncle size. However in the latter, a distinctive adult adoral widening of the siphuncle occurs (see Cichowolski et al., 2015), which does not exist or is not preserved in the specimens described herein. Furthermore, *S. sikus* differs from the two specimens described herein in having a greater angle of expansion. The fragment of an indeterminate bathmoceratid from Darriwilian strata of the San José Formation at Río Yanaorco, Peru, described by Evans (2007), is similar in chamber spacing and general conch outline and possibly synonymous with the specimens described herein. However, because the internal characters of the latter are not known, it is not possible to provide a more detailed comparison.

Order Rioceratida King and Evans, 2019
 Family Rioceratidae Kröger and Evans, 2011
 Genus *Rioceras* Flower, 1964

Type species.—*Rioceras nondescriptum* Flower, 1964, from the Lower Ordovician of New Mexico, southwestern USA; by original designation.

Diagnosis.—Small orthocones; cross sections circular to slightly compressed or depressed; shell smooth; sutures generally straight and directly transverse; camerae shallow with depth 0.1–0.2 mm of dorsoventral diameter of phragmocone; body chamber simple, tubular, or faintly fusiform; septal necks loxochoanitic-orthochoanitic; marginal siphuncle narrow, with segments concave with moderately thick connecting rings; no or strongly reduced endosiphuncular deposits (after Kröger and Evans, 2011).

Rioceras? sp. indet.
 Figure 3.7

Description.—The single specimen consists of a ~25 mm long fragment of a phragmocone. The distance between conch diameters 5–10 mm is 18 mm (angle of expansion is 16°). The outer shell is partly reserved and smooth. The cross section apparently was circular or nearly so. The sutures are straight and directly transverse, at a conch diameter of 8 mm with a spacing of 1.3 mm, and a conch diameter of 10 mm with a spacing of 1.5 mm. At the apical end of the specimen, an impression of the siphuncle is preserved; it has a diameter of ~0.5 mm at a conch cross section of 5 mm and appears to be tubular or nearly so. At a conch cross section of 10 mm, a poorly preserved trace of the siphuncle indicates a siphuncular diameter of ~1.5 mm.

Material.—CPI-10078 (Fig. 3.7), San José Formation, Kimbiri section, bed K-01, *Baltograptus minutus* graptolite Zone, upper Floian, Lower Ordovician.

Remarks.—The poor preservation of the siphuncular characters make determination of this specimen somewhat uncertain because it is unknown if the siphuncular segments were originally tubular, slightly expanding, or slightly concave. However, the relatively narrow marginal and nearly tubular siphuncle is indicative of the Rioceratidae. The straight shell, the nearly circular cross section, and the moderate septal spacing are similar to species of *Rioceras*, although the angle of expansion is relatively large compared with known species of the genus. The specimen is classified in open nomenclature within *Rioceras* because it is known only from a single specimen, revealing limited details of the siphuncle, as well as of the juvenile and adult growth stages.

Family Baltoceratidae Kobayashi, 1935
 Genus *Annbactroceras* Kröger and Evans, 2011

Type species.—*Orthoceras martyi* Thoral, 1935, from the upper Tremadocian of the Montagne Noire, southeastern France; by original designation.

Diagnosis.—Slender, straight to slightly curved, annulated conchs; sutures directly transverse and widely spaced; siphuncle marginal to eccentric in position and closer to the concave side of the conch curvature; septal necks orthochoanitic; siphuncular segments tubular with a diameter 0.1 of the phragmocone diameter (diagnosis after Kröger and Evans, 2011).

Annbactroceras greycostatum (Kobayashi, 1937)
 Figures 3.3–3.6, 3.8, 3.13, 5.2, 5.3

1937 *Cycloceras greycostatum* Kobayashi, p. 434, pl. 8, fig. 4a–c.

Holotype.—*Cycloceras greycostatum*, from ‘Knollenschiefer’ of Obispo, southern Bolivia (Kobayashi, 1937). Listed under PM 01588, Geological Collections of the University of Freiberg, Germany by Kobayashi (1937), but missing from the repositories of the University Museum, University of Tokyo, Japan, and the Geological Collections of the University of Freiberg, Germany (personal communication, Ursula Leppig, Freiburg, 2023).

Neotype.—CPI-10079 (Fig. 3.13), San José Formation, *Baltograptus minutus* graptolite Zone, Floian, Ordovician, Kimbiri section, bed K-01; designated herein.

Diagnosis.—Slightly curved, gradually expanding, annulated longicones with circular conch cross section and angle of expansion of $\sim 8\text{--}10^\circ$; annulated with four or five annuli within a distance similar to the corresponding cross section; distinctiveness of annulations increases with conch diameter; annulations laterally oblique forming broad sinus at antisiphuncular side and broad lobe at prosiphuncular side; additionally ornamented with distinct, irregularly spaced growth lines that trend parallel to the annuli; siphuncle tubular, narrower than one-fourth of corresponding conch diameter; positioned between conch center and concave margin of conch curvature; approximately three or four chambers per distance similar to corresponding conch diameter (diagnosis compiled from Kobayashi, 1937).

Occurrence.—San José Formation, Peru; Capinota Formation, Bolivia.

Description.—The neotype consists of a >73 mm long fragment of the nearly apicalmost parts of the phragmocone. The most apical parts are only preserved as an impression with a diameter of ~ 1.5 mm and a maximum preserved diameter of 11 mm. The angle of expansion of the part ranging from diameter 3–11 mm has an apical angle of 8° . The conch is slightly endogastrically curved (siphuncle positioned closer to the side with concave curvature) with the siphuncle at a distance of 0.5 mm from conch margin where the conch diameter is 3.2 mm. There, the siphuncular diameter is ~ 0.6 mm (relative siphuncular diameter 0.19). The connecting rings are thin and form a barrel-shaped, slightly expanded siphuncle. The shape of the septal neck cannot be determined, due to recrystallization. The chamber length is

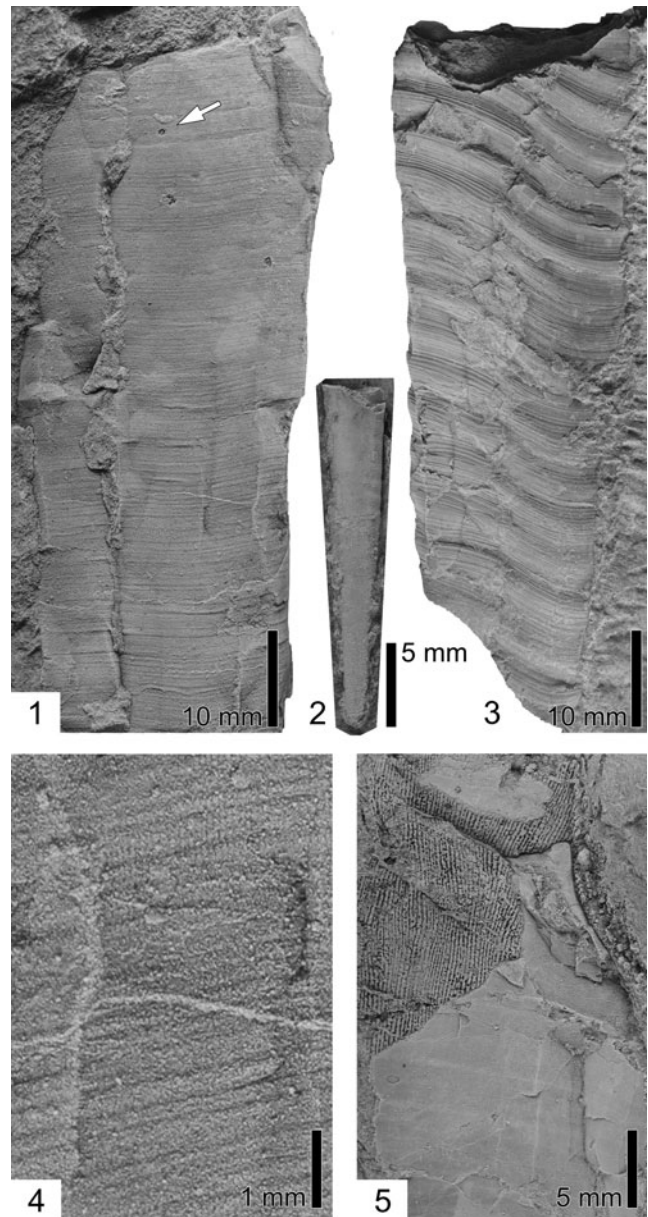


Figure 5. Ornamentation details of cephalopods from the Kimbiri section, Apurímac River valley, Peru, Floian Stage, Ordovician: (1, 4) *Bactroceras coca-folium* n. sp.: (1) CPI-10094, horizon K-01, diagenetically flattened specimen, note the shell borings (arrow); (4) detail of (1). (2, 3) *Annbactroceras greycostatum* (Kobayashi, 1937): (2) CPI-10085, horizon K-02, approximate dorsal view of apical portion; (3) CPI-10081, horizon K-02, lateral view of strongly diagenetically flattened specimen. (5) Indet. cephalopod shell, CPI-10097, horizon K-02, with bryozoan epizoans. All specimens whitened with ammonium chloride.

1.2 mm at a position of 3.3 mm conch diameter (relative chamber length 0.36). The conch is annulated with relatively shallow annuli, which have a distance of 2–3 mm at a conch diameter of 9 mm (relative distance of annuli 0.2–0.3). The amplitude of the annulation decreases toward the apex and the shell is virtually smooth at diameters < 4 mm. The annuli are laterally oblique forming a wide lobe at the prosiphuncular side and a wide sinus over the antisiphuncular side. The conch surface is additionally marked with distinct irregular growth lines, which trend parallel to the annulations.

Specimen CPI-10082 (Fig. 3.5) is a ~20 mm long, slightly diagenetically compressed phragmocone fragment with a diameter of 13 mm. The siphuncle is eccentrically positioned (distance from the conch margin = 0.29 of the corresponding conch cross section), and with a septal perforation with a diameter of 2.2 mm (relative siphuncular diameter 0.17). The annuli are ~3 mm apart (relative distance of annuli 0.23) and form a broad lobe at the prosiphuncular side and a wide sinus at the antisiphuncular side. The septa are deeply concave with a depth of 3 mm.

The largest specimen (CPI-10083, Fig. 3.3, 3.4) is a strongly flattened fragment consisting of a body chamber and likely parts of the phragmocone with a diameter ranging from 14–20 mm along a length of 42 mm (angle of expansion 10°). The internal characters are not preserved, but the conch surface shows the characteristic laterally oblique annulation with ~4 or 5 annulations per distance similar to the corresponding conch cross section and well developed irregularly spaced growth lines.

Specimen CPI-10085 (Fig. 5.2) is a weakly annulated, almost straight apical fragment of a phragmocone, preserving the conch apex. The specimen has a length of 18 mm and a maximum diameter of 3.5 mm (angle of expansion ~11°). At its adoral end, a septum is preserved with a septal perforation of 0.6 mm in diameter (relative siphuncular diameter ~0.17). The septal perforation is slightly eccentrically positioned at a distance 1.1 mm from conch margin. The apex is straight, blunt to hemispherical, and without a distinctive apical constriction.

CPI-10086 is very similar to CPI-10085 and has a diameter of 3.7 mm. Traces of a siphuncle with a diameter of 0.6 mm are preserved at a distance of 0.8 mm from the conch margin.

Materials.—CPI-10079 (neotype) and CPI-10080 from the Kimbiri section bed K-01; seven additional specimens from bed K-02 (CPI-10081–10086) and K-11 (CPI-10087). Four specimens (CPI-10088–10091) from LIB. All from *Baltograptus minutus* graptolite Zone, Floian, Ordovician.

Remarks.—The combination of a moderate angle of expansion and the presence of a relatively deep broad ventral lobe distinguishes this species from *Annbactroceras martyi* (Thoral, 1935). The latter has a very low angle of expansion (5° or less). *Annbactroceras felinense* Kröger and Evans, 2011 has a marginal siphuncle.

The holotype is missing (see above) and the only stratigraphic information given by Kobayashi (1937, p. 434) is ‘Knollenschiefer’ of Obispo, which probably refers to the ‘Geodenschiefer’ of Steinmann and Hoek (1912, p. 200) and has been interpreted as the Capinota Formation (Evans, 2007). This unit is poorly age constrained, ranging from Floian to Darrivilian (González Bonorino and González Bonorino, 1994; Egenhoff et al., 2007).

Genus *Bactroceras* Holm, 1898

Type species.—*Bactroceras avus* Holm, 1898, from the Darrivilian of Öland, Sweden; subsequent designation by Glenister (1952, p. 90).

Bactroceras cocafolium new species
Figures 3.9, 3.10, 5.1, 5.4

Holotype.—CPI-10092 (Fig. 3.9, 3.10), San José Formation, Kimbiri section, bed K-02, *Baltograptus minutus* graptolite Zone, upper Floian, Lower Ordovician.

Diagnosis.—Slightly endogastrically curved longicones with circular conch cross section and angle of expansion ~7°; ornamented with a fine reticulate pattern of transverse and longitudinal lirae with a distance of ~0.1 mm; transverse lirae form a wide and shallow lobe on the prosiphuncular side; siphuncle marginal with a diameter of ~0.18 mm of the corresponding conch cross section.

Occurrence.—San José Formation, *Baltograptus minutus* graptolite Zone, Floian, Ordovician, Kimbiri section north of the village of Kimbiri Alto, along the trail parallel to the Kashiroveni stream (Fig. 2, loc. 3). Geographical coordinates for the type locality and stratotype K-02 are 12°34'53.6"S, 73°44'42.9"W.

Description.—The holotype is a 20 mm long phragmocone fragment with a circular conch cross section of 10.5–13 mm (angle of expansion ~7°). The conch surface is ornamented with fine rounded growth lines or transverse lirae (~10 per 1 mm) and delicate longitudinal lirae (~10 per 1 mm). The transverse lirae form a wide and shallow lobe over the prosiphuncular side of the conch. On its adapical end, a septum is preserved and runs directly transverse with a concavity of ~4 mm. The marginal septal perforation has a diameter of 1.8 mm (relative siphuncular diameter ~0.18).

Specimen CPI-10094 (Fig 5.1, 5.4) is a strongly taphonomically compressed fragment of the conch. The maximum diameter of this specimen is 14 mm, and it has a well-preserved reticulate ornamentation of 0.1 mm spaced transverse and longitudinal lirae.

The apical parts are partly preserved in one specimen (CPI-10093a-b; Fig. 3.12). There, the siphuncle is marginally positioned, and the conch has a diameter of ~5 mm at a distance of 22 mm from the tip (angle of expansion ~7°). The conch appears to be slightly curved with the siphuncle on the concave side of the conch curvature. The apex is apparently blunt to hemispherical, without distinctive apical constriction, and is ornamented with rounded transverse lirae that have a distance of ~0.1 mm.

Etymology.—Named after the coca plant (*Erythroxylum coca* Lamarck, 1786) and *folium* (Lat., neutral gender), its leaves. The name refers to the coca crops that support many farmers in the Apurímac River valley.

Materials.—CPI-10092 (holotype) and one additional specimen (CPI-10093a-b, part and counterpart) from bed K-02; two specimens from bed K-01 (specimens CPI-10094, 10095). All from Kimbiri section, *Baltograptus minutus* graptolite Zone, Floian, Ordovician.

Remarks.—The only known species of *Bactroceras* with a fine reticulate ornamentation is the Late Ordovician *Bactroceras interpolatum* (Barrande, 1867), which differs in having a narrow, submarginal siphuncle with a relative siphuncular diameter of only 0.1 mm (see Aubrechtová, 2015).

Order, family, genus, and species indet.

Figure 6

Description.—The specimen consists of an internal mold of a body chamber fragment that includes the last septum of the phragmocone. The conch has a circular cross section with a diameter ranging from 44–62 mm along a length of 82 mm (angle of expansion $\sim 13^\circ$) and reaches a maximum diameter of 67 mm; it is slightly curved with the siphuncle near the convex conch margin. The conch surface is not preserved; the mold is smooth without traces of ornamentation. At the base of the body chamber, a narrow contact band of the last septum with the external conch is visible (1.2 mm wide at venter). The suture is directly transverse and forms a very shallow marginal lobe and a deep (4.2 mm) U-shaped ventral lobe. The septal perforation is marginal and with circular cross section of 13 mm with traces of the septal necks only partly preserved indicating a length of at least 1 mm. The septal curvature has a depth of 3 mm.

Material.—CPI-10096, from a nodule from bed CB-87, Inambari River section, San José Formation, southeastern Peru.

Remarks.—The fragmentary character of the specimen does not allow for a more precise determination. However, the

relatively large size, the large marginal siphuncle (septal perforation is 0.3 of conch diameter), and the shape of the preserved parts of the septal neck suggest that it belongs to an endoceratid. The relative narrow shape of the ventral lobe, which is part of an otherwise nearly straight transverse suture line, distinguishes the specimen from species assigned to *Cyrtendoceras* Ulrich and Foerste, 1936 and *Belloceras* Cecioni, 1965, by Cecioni (1965), and is suggestive of *Protocyrtendoceras* Cecioni, 1965. The last genus, which is known from middle Tremadocian to Floian strata of Argentina (Cichowolski et al., 2023) differs in having a straight shell (see review by Cichowolski, 2009).

Discussion

The composition of the cephalopod assemblage of the Floian portion of the San José Formation is typical for pelagic depositional environments given the dominance of small orthoceratids, e.g., rioceratids and baltoceratids (see Kröger et al., 2009 and references therein). Floian assemblages from similar depositional environments have been described from the Pircancha Formation, Bolivia (Aubrechtová, 2015), from the Montagne Noire, France (Kröger and Evans, 2011), from England and Wales, UK (Evans, 2004), and from Spitsbergen, Norway (Kröger and Pohle, 2021). The occurrence of genera in the



Figure 6. Cephalopod, order, family, genus and species indet., mold of a body chamber, CPI-10096, from a nodule from Inambari River section, Peru, Floian Stage, Ordovician: (1) lateral view, venter toward right; (2) ventral view; (3) lateral view, venter toward left. Scale bar = 10 mm. Whitened with ammonium chloride.

San José Formation with global or very widespread paleogeographical ranges, e.g., *Bactroceras* and *Rioceras*, therefore, can be partly explained by paleoecology, i.e., representing a predominantly pelagic habitat. However, *Annbactroceras*, *Rioceras*, and *Saloceras*, which occur also in the San José Formation, are absent in Spitsbergen, and are important elements not only in pelagic depositional environments, but in more proximal settings, e.g., the siltstone of the Upper Fezouata Formation, Morocco (Kröger and Lefebvre, 2012) and the upper Acoite Formation, Argentina (Cichowolski et al., 2015). These latter taxa display a clear peri-Gondwana-Avalonia paleogeographic affinity for the Peruvian assemblage, which is in alignment with the distribution of brachiopods (Gutiérrez-Marco and Villas, 2007), conodonts (Gutiérrez-Marco et al., 2008), and trilobites (Hughes et al., 1980).

The co-occurrence of *Annbactroceras greycostatum* in the Peruvian strata of the San José Formation and in nodular shales of Obispo, southern Bolivia reflects their paleogeographical proximity within the Central Andean Basin. Furthermore, it could help constrain the age of the Capinota Formation to which the Obispo sequence has been correlated (Evans, 2007). If true, this would give further evidence that the lower portion of this formation ranges into the late Floian (e.g., González Bonorino and González Bonorino, 1994).

The occurrence of *Annbactroceras greycostatum* therefore contributes toward a more complete picture of the Floian fauna of the Central Andean Basin. This fauna, which contains benthic species, e.g., brachiopods (e.g., *Notorthisina* Havlíček and Branisa, 1980, *Paralenorthis immitatrix* Havlíček and Branisa, 1980), trilobites (e.g., *Branisaspis speciosa* Přibyl and Vanek, 1980, *Hoekaspis* Kobayashi, 1937), and planktic graptolites (see e.g., Gutiérrez-Marco et al., 2008; Benedetto et al., 2009), displays a distinct west Gondwanan signature (e.g., Benedetto et al., 2009; De la Puente and Rubinstein, 2013).

No apparent species overlap occurs between our Floian assemblage and the assemblage described by Evans (2007) and collected by Douglas (1933) from the San José Formation in Yanaorco River area, eastern Peru. As noted by Evans (2007), this latter assemblage likely represents Middle Ordovician strata within the San José Formation and thus is considerably younger than the assemblage described herein. However, it can be correlated with certain Darriwilian specimens from the Nueva Alianza locality NA-3 (like an unfigured Eothinoceratidae gen. indet. sp. indet. collected by JCG-M, which is virtually identical to a similar specimen described by Evans, 2007, figs. 2A, 4F) and with undescribed material with fine transverse ornamentation derived from Darriwilian strata of the Inambari River section (unpublished data, B. Kröger and J.C. Gutiérrez-Marco, 2023, derived from the middle part of the San José Formation).

Conclusions

A cephalopod assemblage, collected from the Floian section (*Baltograptus minutus* graptolite Zone) of the San José Formation of the Kimbiri area, northwest of Cuzco, southeastern Peru allows for an initial report of Ordovician cephalopods with species-level determinations from this area. The assemblage contains five species of small orthoceracones belonging

to four families of three orders: one indeterminate dissidocericid, one bathmoceratid (*Saloceras* sp. indet.), one rioceratid (*Rioceras?* sp. indet.), and two baltoceratids (*Annbactroceras greycostatum*, *Bactroceras cocafolium* n. sp.). An additional indeterminate cephalopod is described from nodules within the San José Formation from the Inambari River in southeastern Peru. The assemblage, with its orthoceracone, baltoceratid dominance, represents a typical Floian pelagic cephalopod fauna. *Annbactroceras greycostatum* is known from the Capinota Formation, Obispo region, Bolivia, which together with the Coroico Formation, are correlated with the San José Formation in its eastward extension to Bolivia within the northern sector of the Central Andean Basin (e.g., Suárez-Soruco, 1992; Mitchell et al., 2008). The other taxa indicate a peri-Gondwana-Avalonia paleogeographical relationship of the cephalopod fauna. This is coherent with previously published data from brachiopods and trilobites (Hughes et al., 1980; Gutiérrez-Marco and Villas, 2007).

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Author contributions

The material for this study was collected by JCG-M and identified by BK. The manuscript was written by BK and JCG-M. CAC extensively discussed scientific literature and details of local geology with JCG-M and improved the manuscript. All authors read and commented on the final version of the manuscript.

Declaration of competing interests

The authors declare none.

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