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New paleontological and geological data on the Ordovician and Silurian of Bolivia

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Abstract — The oldest vertebrates of South America are from the thick Anzaldo (=Cuchupunata) Formation in central Bolivia. At the scale of the basin, the Anzaldo is overlain by the San Benito, Tokochi, Cancañiri, Llallagua and Kirusillas/Uncía formations. The Anzaldo was classically dated Caradoc (early Late Ordovician), but recent paleontological data have suggested a Llanvirn age (early Middle Ordovician). The only significant fossil invertebrates recently collected in the Anzaldo, viz., lingulid brachiopods, give an age not older than Late Ordovician. Fossils from the Tokochi suggest a Caradoc age. The microfossils (acritarchs and foraminifers mainly) collected in the Cancañiri and Kirusillas/Uncía formations indicate an Ashgill to Wenlock age (late Late Ordovician to late Early Silurian) for these formations. A Caradoc (or perhaps older) age thus seems more correct for the Anzaldo Formation. These new paleontological data have major implications on our knowledge of the Ordovician-Silurian basins of Bolivia: 1) transition from a Middle Ordovician marine foreland basin to a Late Ordovician-Llandovery glacial-marine to turbidite trough in the Altiplano occurred in the (late?) Caradoc; 2) a major sea-level rise developed around the Llandovery-Wenlock boundary; 3) a fossiliferous limestone member of shallow origin and early Wenlock age is present approximately between Cochabamba and Santa Cruz.

Resumen — Los vertebrados más antiguos de Sudamérica provienen de la espesa Formación Anzaldo (= Cuchupunata) de Bolivia central. A la escala de la cuenca, la Formación Anzaldo subyace a las formaciones San Benito, Tokochi, Cancañiri, Llallagua y Kirusillas/Uncía. Datos paleontológicos recientes han sugerido una edad llanvirniana (Ordovícico medio temprano) para la Formación Anzaldo tradicionalmente asignada al Caradociano (Ordovícico superior temprano). Según el presente estudio, los únicos invertebrados fósiles significativos de la Formación Anzaldo son braquiópodos lingúlidos, que indican una edad no mayor que Ordovícico superior. Fósiles de la Formación Tokochi sugieren una edad caradociana (superior?). Los microfósiles (principalmente acritarcos y foraminíferos) recolectados en las formaciones Cancañiri y Kirusillas/Uncía indican edades que van del Ashgilliano al Wenlockiano (Ordovícico superior tardío a Silúrico inferior tardío) para estas unidades. Por lo tanto, una edad caradociana (o quizás más antigua) parece más correcta para la Formación Anzaldo. Estos nuevos datos paleontológicos tienen importantes implicancias para nuestro conocimiento de las cuencas ordovícicas y silúricas de Bolivia: 1) la transición de una cuenca marina de antepaís en el Ordovícico Medio a una fosa glacio-marina a turbidítica ubicada en el Altiplano en el Ordovícico Superior-Llandoveriano ocurrió en el Caradociano (superior?); 2) un ascenso mayor del nivel marino se desarrolló alrededor del límite Llandoveriano-Wenlockiano; 3) un miembro calcáreo fosilífero de ambiente somero y edad Wenlockiano inferior está presente aproximadamente entre Cochabamba y Santa Cruz.

INTRODUCTION (PYG & AB)

Ordovician vertebrates, the oldest true vertebrates known in the fossil record, are rare. They have been collected in Australia and in both North and South America (Elliott *et al.*, 1991). In South America, they are known from Bolivia by a single species: *Sacabambaspis janvieri* Gagnier, Blieck and Rodrigo (1986) from the Anzaldo Formation in the central part of the Cordillera Oriental of Bolivia and by fragmentary remains north and south of this area [*Andinaspis suarezorum* Gagnier (1991), supposedly from the Ordovician Capinota Formation, is of doubtful stratigraphic origin and probably a Devonian fossil; see below].

However, since the discovery of *Sacabambaspis*, the question of its exact age has grown (see reviews by Gagnier, 1991, 1993). *Sacabambaspis* is considered as phylogenetically related to the Australian species *Arandaspis prionotolepis*, which was collected from probably early Llanvirn sandstones (Webby, 1981; see discussions by Ritchie and Gilbert-Tomlinson, 1977). This, however, does not mean that *Sacabambaspis* is as old as *Arandaspis*. The Anzaldo Formation, from which *Sacabambaspis* was collected, is considered either Caradoc or Llanvirn-Llandeilo in age (Cuchupunata is another name frequently used for the same formation, but Anzaldo has priority — see arguments *in* Gagnier, 1991, 1993). It has been thought to be Caradoc in age (Suárez Soruco, 1976; Rodrigo and Castaños, 1978; Aceñolaza, Baldis *et al.*, 1987), and this age was accepted by Gagnier *et al.* (1986). However, recent data have suggested an older age. Toro *et al.* (1990b) indeed mention, but do not figure, a faunal association of trilobites and conodonts in at least one vertebrate-bearing locality: the trilobite *Homalonotus (Brongniartella) bistrami* [which probably corresponds to *Brongniartella zaplensis*], associated to *Hoekaspis schlagintweiti,* would indicate a Llanvirn age. *Hoekaspis*, associated to *Synhomalonotus kobayashii* in another locality of the Anzaldo Formation, is early Llanvirn. The conodonts from the same localities *(Neocoleodus, Drepanoistodus, Plectodina, Phragmodus*; Toro *et al.*, unpublished report, *in* Gagnier, 1991, 1993) would however be less significant since some genera indicate only the Middle and Late Ordovician.

The 1991 National Geographic Society expedition "South American Ordovician Vertebrates" was organised with the purpose to find new evidence to date more precisely these supposedly "oldest" vertebrates. Another goal of the same expedition concerned *Andinaspis suarezorum*. This species is represented by a single, poorly preserved fragment, collected at the Geological Survey of Bolivia locality GEOBOL 5011, "in 'undifferentiated' Ordovician strata currently referred to the Capinota Formation, of Llanvirn age (early Middle Ordovician)", 8.5 km SE of Morochata, Ayopaya Province, Cochabamba Department (Gagnier, 1991). We also prospected this locality in 1991, as well as the Iglesiani valley: all the fossiliferous sites that we could find in the Paleozoic rocks, below the Cretaceous-Tertiary sediments, failed to yield any vertebrate remains, but did yield many invertebrates and spores indicative of a Devonian age. So, if *Andinaspis* really comes from this locality, it is not Ordovician in age, and we do not deal with it here (see Blieck *et al.*, in press).

The abbreviations used hereafter are: km, kilometers; m, meters; Ma, megaannum or millions of years, a point in time; Myr, millions of years, a duration of time. YPFB is the national Bolivian oil company Yacimientos Petrolíferos Fiscales Bolivianos, and Orstom is the Institut Français de Recherche Scientifique pour le Développement en Coopération.

GEOLOGICAL SETTING (TS)

Geological context

The Bolivian Andes (Fig. 1) provide numerous and excellent exposures of Phanerozoic strata, principally of Paleozoic age, because Andean thrust deformation has considerably propagated into Bolivia, from the Late Oligocene to the present, by taking advantage of several potential décollement levels located in thick Paleozoic shale units (Sempere *et al.*, 1989, 1990). In the Bolivian orocline area, there is a close control on the geometry of Andean deformations by the geometry of the Paleozoic basin and sedimentary pile (Sempere *et al.*, 1991a).

During most of Late Ordovician to Paleogene times, Bolivia roughly occupied the southern part of a longitudinal subsident domain (the Bolivia-Peru basin) which ran parallel to the Pacific margin of South America and remained bounded southwards by the Sierras Pampeanas area in northwestern Argentina. An important consequence of this paleogeographic feature is that, from Late Ordovician to Early Paleocene times, the marine transgressions reached Bolivia from the northwest (Sempere, in press).

The boundary faults of the tectonostratigraphic domains distinguished in Bolivia (Sempere *et al.*, 1988) appear in Fig. 1 because these domains were displaced and shortened, sometimes considerably, during the Andean orogeny, which is crucial for a good understanding of paleogeographies. Furthermore, the southern half of Andean Bolivia is crossed by a NE-striking major structural element, called the Khenayani-Turuchipa paleostructural corridor (CPKT; Fig. 1), which appears to have largely controlled both Phanerozoic sedimentation and deformation in southwestern Bolivia (Sempere *et al.*, 1991a).

General stratigraphy

The Paleozoic stratigraphic record of Bolivia is practically complete and one of the richest in the Andes. Many units are fossiliferous, and its chronostratigraphy is fairly known. However, it is not always well constrained in detail, and more biostratigraphic, geochronologic and sequential stratigraphic works are still needed. This paper provides some new data about the Ordovician and Silurian periods.

The basement of the Phanerozoic series in Andean Bolivia consists of Late Proterozoic or Early Cambrian rocks, but crops out only in a few spots, i.e., in the Tarija area, along the Chapare road northeast of Cochabamba, and at Cerro Chilla south of Lake Titicaca.

Present state of knowledge of the Bolivian Phanerozoic stratigraphy distinguishes eight main periods. The stratigraphic units dealt with in this paper belong to the Tacsara supersequence (Late Cambrian-middle? Caradoc, ≈80 Myr or more), and to the Chuquisaca supersequence (late Caradoc?-middle Famennian, ≈85 Myr). The boundary between these two supersequences is generally sharp (Sempere, in press), but it can only exceptionally be described as an unconformity (as is the case in the northwestern Argentine Puna). Both supersequences are of marine origin.

The main lithologies of Early Paleozoic strata include sandstones (generally quartzitic), siltstones, mudstones and shales, with diamictites (Ashgill), minor conglomerates (Cambrian, Ashgill), and very rare calcareous beds (Middle Ordovician, early Wenlock). Depositional environments grade from coastal and shallow-marine to slope and basinal.

The Early Paleozoic series of Bolivia is thick (over several thousand meters), and provides a good record of the evolution of this part of western Gondwana. These mostly siliciclastic deposits apparently accumulated in a tectonic context controlled by the proximity of a passive margin from Middle Cambrian to Middle Ordovician time, and in a wide back-arc setting related to an active margin afterwards (Sempere, 1992, in press). Specific eustatic events are recorded: some noteworthy black shale units, as in the late (?) Caradoc (Tokochi Formation) and Early to Middle Silurian (Kirusillas/Uncía formations), indicate maximum transgressive episodes. Invasions of prograding sands, as in Caradoc and Pridoli times, suggest rapid colmatation of the basin in relation with relative sea level falls. A glacial-marine episode of Ashgill age (Cancañiri Formation) is well recorded.

Late Cambrian — middle? Caradoc evolution

While North America separated from South America in latest Proterozoic and/or Early Cambrian time and subsequently drifted northwestwards (Bond *et al.*, 1984; Murphy and Nance, 1991), the western margin of Gondwana evolved as a passive margin, with a large-scale dextral shear component. This led to the formation, in Middle to Late Cambrian time, of the Puna aulacogen, above a thinned, rifted crust (Fig. 1). These tensional conditions also favored the installation of a wide marine epicontinental basin along the proto-Andean domain, which was the locus of thick sedimentation.

An important geodynamic upheaval occurred in Middle Ordovician time and the southern Iapetus-Gondwana margin became active, probably with a sinistral shear component at the latitude of Bolivia. A magmatic arc appeared, separating a fore-arc from the wide marine back-arc basin, inside which most part of Andean Bolivia is presently located. Closure and deformation of the Puna aulacogen propagated from the west, starting near the Arenig-Llanvirn boundary (according to data displayed by Bahlburg, 1990), and produced the Ocloyic belt of the Argentine-Chilean Puna and southwestern Bolivia. The rest of the previous depositional area, including the Cochabamba area, evolved as the marine foreland basin of this deformation, which apparently continued well into Caradoc time. The development of the Ocloyic deformation was apparently coeval with the Taconic deformation of the symmetrical margin of eastern North America and of the northern Andes. Development of roughly synchronous major compressional deformations on both sides of the southern Iapetus ocean suggests that a major global plate reorganization occurred in Middle Ordovician time (Sempere, 1992, in press).

Strata of Late Cambrian to middle (?) Caradoc age widely crop out in the Cordillera Oriental of Bolivia, as well as in the southern Altiplano and in some parts of the Subandean belt. They are unknown in the Ulloma-Coipasa-Uyuni domain (UCU, Fig. 1), where the oldest outcropping rocks are Late Proterozoic and/or Early Cambrian (with a Late Cretaceous cover) in the north, and the Ashgill-age Cancañiri Formation in the center and south. The base of this Tacsara supersequence is known in the Tarija area, where the exposures are excellent, and along the Cochabamba-Chapare road, where they are poor and heavily faulted. However, in most of the Cordillera Oriental, the basal décollement of the Andean thrusts is located in Early to Middle Ordovician shales, and no older strata are exposed. In all areas, the successions are thick and monotonous.

In southwestern Bolivia (Tarija area), the sequence

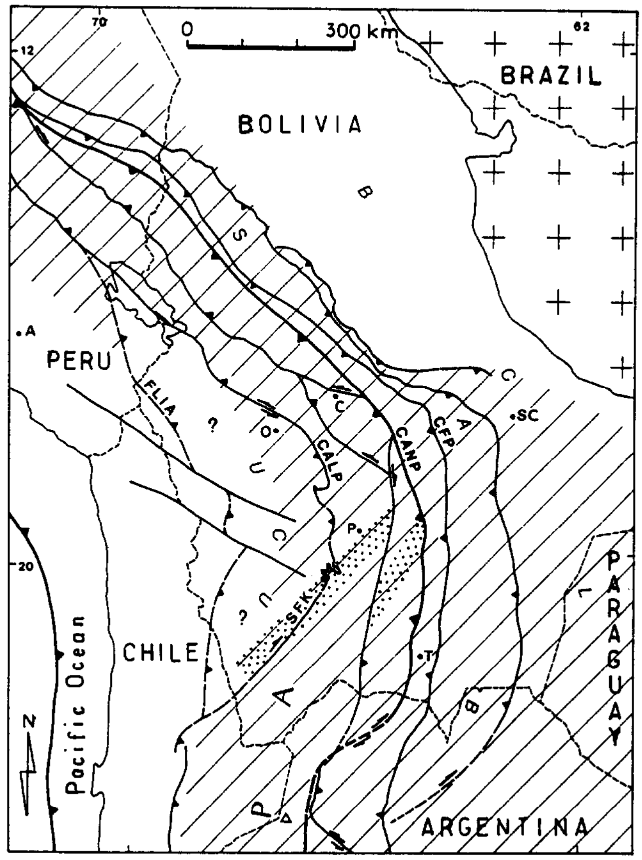

Fig. 1. General structure of Bolivia and neighbouring regions. Hatched = approximate maximum extent of Ordovician to Middle Silurian basins; crosses = Guaporé shield; dotted = CPKT (Khenayani-Turuchipa paleostructural corridor); fine dashed lines = national boundaries. Abbreviations for geologic elements and domains (most are Spanish): CALP = Main Altiplanic thrust, CANP = Main Andean thrust, CFP = Main Frontal thrust, FLIA = Intra-Andean Boundary fault (conjectural), SFK = Khenayani fault system; BCL = Beni-Chaco lowlands, PA = Puna aulacogen, SAB = Subandean belt, UCU = Ulloma-Coipasa-Uyuni domain. Abbreviations for cities: A = Arequipa, C = Cochabamba, O = Oruro, P = Potosí, SC = Santa Cruz, T = Tarija. Δ = sampling location of Llandovery-age fauna of warm-water affinity at Cerro Rincón, Argentina (Isaacson *et al.*, 1976).

begins with shallow-marine clastics, which grade to open-marine thick graptolite shales intercalated with subordinate turbidites and slumps. This Late Cambrian-Llanvirn sequence is affected in this area by the Ocloyic deformation, which is post-dated in northernmost Argentina by beds of Ashgill and Llandovery age (Isaacson *et al.*, 1976; Benedetto *et al.*, 1992). The Ocloyic deformation shows an increase in intensity from east to west, but is not known north of lat. 20°S.

North of lat. 20°S, the exposed succession consists of a thick shallowing-upward sequence of Llanvirn to Caradoc age, which is conformably capped by the late Caradoc (?) Tokochi Formation and/or the Ashgill Cancañiri Formation. In the Cochabamba area, it includes, from base to top, the Capinota (grey to dark shales with some sandstone intercalations), Anzaldo (sandstones, siltstones and mudstones) and San Benito (quartzitic sandstones with subordinate siltstones) formations (Fig. 2). These units grade vertically and laterally into each other, and hence are *not* separated by sharp contacts, nor time lines. Deposition of these thick shallow-marine siliciclastic strata during most part of Llanvirn-Caradoc time in central to western Bolivia was coeval with the development of the Ocloyic deformation in southwesternmost Bolivia and northwestern Argentina. These thick and monotonous sandstone-siltstone intercalations are therefore interpreted as the fill of the marine foreland basin which formed in relation with this deformation (Sempere, 1989, 1992, in press).

Late Caradoc? — Silurian evolution

The Tokochi and Cancañiri formations (Fig. 2) belong to the first stratigraphic set of the Chuquisaca supersequence (late Caradoc?-middle Famennian). This set of units spans the late Caradoc?-middle? Llandovery time interval and includes the Tokochi, Cancañiri and Llallagua formations (Fig. 2), which all reach their known maximum thickness in the eastern UCU domain, whereas they rapidly thin out to the southeast and east. In the Cochabamba area, the Tokochi and Llallagua formations are absent, whereas the Cancañiri is only a few tens of meters thick and is sharply overlain by the Kirusillas/Uncía Formation.

Where present, the Tokochi Formation (Sempere *et al.*, 1991b) consists of black, pyrite- and organic-rich shales, up to 200 m-thick, which overlie apparently shallow-marine Caradoc strata. This recently defined unit is thought to mark a sea level high, which might be used for its correlation at a global scale, and to have been deposited in a relatively deep, anoxic environment. It has only

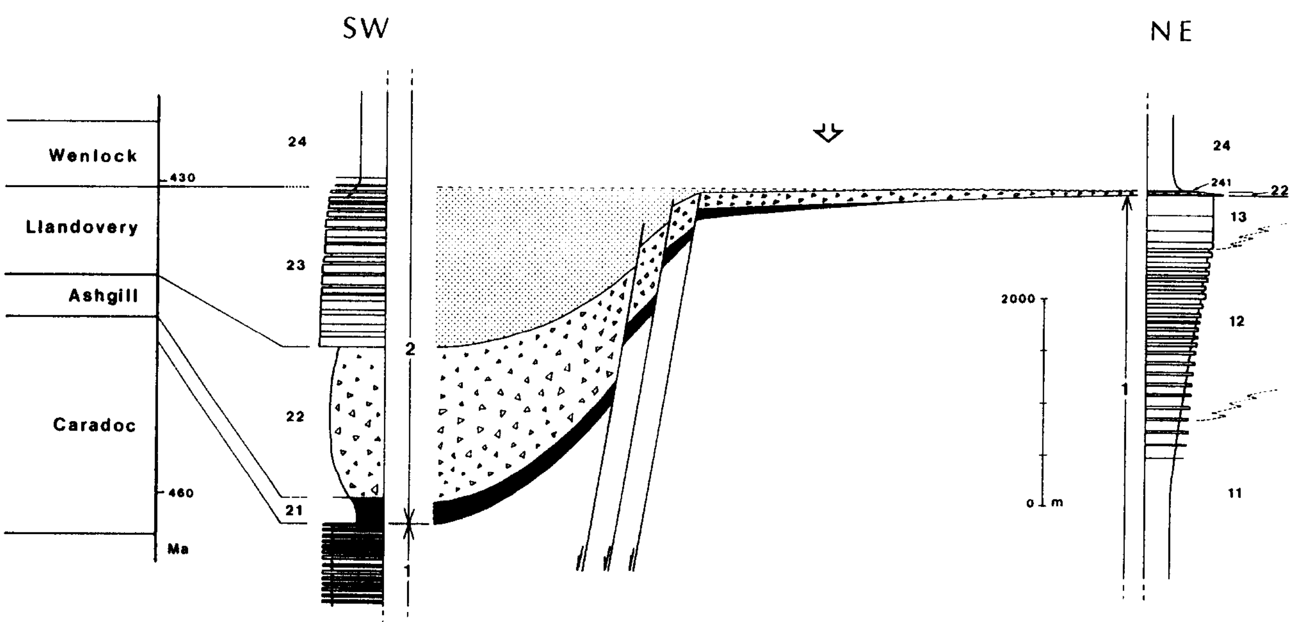

Fig. 2. Schematic spatial relationships and current chronostratigraphic attributions for the units dealt with in this paper. The Yura-Ticatica area, 70 km southwest of Potosí, is type of SW section, whereas the Cochabamba area is type of NE section. Stratigraphic units: 1 = Tacsara supersequence (late Cambrian-middle? Caradoc; mostly mudstones, siltstones and sandstones), 11 = Capinota Formation (mainly shales), 12 = Anzaldo Formation (mudstone-siltstone-sandstone intercalations), 13 = San Benito Formation (mainly quartzitic sandstones); 2 = Chuquisaca supersequence (late Caradoc?-middle Famennian), 21 = Tokochi Formation (black shales), 22 = Cancañiri Formation (mostly mud-dominated diamictites), 23 = Llallagua Formation (mainly thick-bedded sandstones), 24 = Kirusillas (NE) / Uncía (SW) formations (mainly dark to olive-green shales), 241 = Sacta limestone member of the basal Kirusillas/Uncía Formation. See text for data about chronologic attributions. Time scale from Harland et al. (1990). The lowermost part of the Kirusillas/Uncía Formation is roughly considered as a basal transgressive surface and arbitrarily held horizontal (dashed line). See Fig. 5C for detailed section illustrating the San Benito — Cancañiri — Kirusillas relationships and thicknesses in the Cochabamba area. Vertical arrow shows schematic paleogeographic location of Río Blanco section. Area of main synsedimentary (Cancañiri-Llallagua depositional time) normal faulting is schematic, and would very roughly correspond to present-day CALP-SFK system (Sempere et al., 1991a, b; Sempere, in press). No horizontal scale because of schematic restoration of paleogeographic cross-section.

yielded an open-marine fauna, namely orthocere cephalopods and the Caradoc-age (?) pseudoplanctonic brachiopod *Schizocrania filosa* (L. Branisa, pers. comm.). On a global scale, it possibly correlates with Caradoc or late Caradoc black shale units marking a sea level high, as the ones documented in eastern Canada by Hiscott *et al.* (1986) and Schenk (1991).

There may be locally some rapid transition between the Tokochi and Cancañiri formations. The latter mainly consists of greenish grey, poorly bedded to unstratified, mostly resedimented sandy mudstones and diamictites (mass flows), and minor sandstones (basinal turbidites; iron-rich shelf and near-shore clastics in the proximal, northeastern and southern parts of the basin). The Cancañiri Formation is of Ashgill age (Sempere, 1990; Toro *et al.*, 1991, 1992; Benedetto *et al.*, 1992), but its top is possibly earliest Llandovery, and its lower part possibly late Caradoc. Its thickness can reach 1500 m or more in the eastern UCU domain (Fig. 1). The clasts, millimetric to metric in size, include subrounded to angular pieces of quartzite, sandstone, shale, quartz, and rarer igneous rocks (Rodrigo *et al.*, 1977; Suárez Soruco, 1977). In basinal to intermediate localities, clast size apparently increases upsection. Rounded sandstone clasts of cobble to boulder size sometimes bear a Late Ordovician fauna (Havlicek and Branisa, 1980). Some quartz and igneous clasts are clearly faceted and striated, indicating that they proceeded from a penecontemporaneously glaciated area. Sandstone olistoliths are present, being bigger (up to 1000 m^3) and more abundant near the CPKT, which suggests that this structural element was active during deposition of the Cancañiri, producing fault scarps and block sliding (Sempere *et al.*, 1991a, b). The Cancañiri Formation is interpreted to have been deposited during a period of regional tensional tectonic activity, which produced a high rate of resedimentation, while a large part of Gondwana was glaciated (Sempere, in press). The climate was probably cool to cold, with possibly some short warm interglacial periods which would have permitted the deposition of ferruginous sandstone intercalations.

The "Huanuni Formation" is a very micaceous siltstone unit which gradationally overlies the more classic Cancañiri facies in several areas of Bolivia. Its vertical and lateral relationships indicate that it should be best considered as an upper member or facies of the Cancañiri Formation, and not as a distinct unit (Sempere, 1990).

The Llallagua Formation overlies the Cancañiri Formation with a sharp discontinuity (Fig. 2). It practically only exists west of the CALP-SFK system, where it consists of whitish coarse to medium sand turbidite beds, one to several meters-thick, and subordinate siltstones and mudstones, and can reach a thickness of 1500 m or more in the eastern UCU domain (Fig. 1). It transitionally grades to the Uncía (Kirusillas) Formation, and forms with this unit a thinning- and fining-upward succession. The Llallagua is attributed to the Llandovery because of its stratigraphic position. Because of its vertical, and thus lateral, transition to the Uncía Formation, its upper part must be a time-equivalent of the basal Kirusillas (=Uncía) Formation more to the east (Fig. 2), which has yielded a late Llandovery graptolite (*Monograptus turriculatus*; Branisa *et al.*, 1972). East of the CALP-SFK system (see Fig. 1), as in the Cochabamba area, the Kirusillas/Uncía Formation directly overlies the Cancañiri Formation, by means of a discontinuity which appears to mark a depositional hiatus and/or a regional erosional surface that would have developed during part of the Llallagua depositional time. This discontinuity is documented by the data presented below, and in Fig. 5C.

Several lines of evidence suggest that deposition of the late Caradoc? to Llandovery strata occurred in a basin controlled by active normal faulting (see Fig. 2). Contemporaneous facies succession was induced by a major glacio-eustatic sea-level low (Cancañiri Formation, Ashgill ice age) which developed between two maximum transgressive episodes (Tokochi and lower Kirusillas/Uncía Formations), albeit in a tectonically active context. The mostly resedimented Cancañiri and Llallagua Formations are interpreted to represent lower and upper lowstand deposits, respectively (Sempere, in press).

The late Llandovery-middle Famennian set includes many units which are found, under different names, in the Bolivian Andes, Subandean belt and Beni-Chaco plains. Shallow-marine, relatively warm-water faunas are known as early as Llandovery (Isaacson *et al.*, 1976) and early Wenlock (Branisa *et al.*, 1972; Merino Rodo, 1991) times in marginal localities of the central Andean basin. A thin limestone unit of early Wenlock age (Sacta limestone; Merino Rodo, 1991, and pers. comm.) intercalates in the basal portion of the late Llandovery-Ludlow dark shales of the Kirusillas/Uncía Formation in the lowland and mountain area between Cochabamba and Santa Cruz. It is even directly transgressive upon the pre-Ordovician basement just north of the Subandean foothills in this area (YPFB, unpublished data). As evidenced in this paper, this limestone member also exists at the base of the Kirusillas/Uncía Formation in the Río Titiri area about 15 km northwest of Cochabamba, as at Cuatro Esquinas (see below, and Pérez Guarachi, 1989).

The Silurian was a time of onlap of sedimentation toward the northeast. Decrease and geographic homogeneization of subsidence in ≈Llandovery time are interpreted to mark a change in tectonic regime: whereas the late Caradoc?-middle? Llandovery stratigraphic set is thought to have been deposited through the creation and activity of a wide extensional trough (roughly coinciding with the UCU domain), the late Llandovery-middle Famennian set is interpreted to have been deposited in a large marine "foreland" basin related to sinistral transpressional activity of the Gondwana margin (Sempere, in press).

STRATIGRAPHY (AB, CCE, PYG & DV)

Anzaldo Formation

Ten Ordovician vertebrate-bearing localities are now known from this ca. 2000 m-thick formation: Sacabamba (the type-locality of *Sacabambaspis*), Anzaldo (the type-locality of the formation), Sacabambilla, Cochabamba (Cerro San Pedro) and Santiváñez [Gagnier *et al.*, 1986; Gagnier, 1987, 1989, 1991; Gagnier and Blieck, 1992]; Cuatro Esquinas (Río Millu Mayu) and Calientes (Cerro Lloja Pata Punta) from which Toro *et al.* (1990b) mention fish fragments associated to lingulids, conodonts and trilobites; and three localities which were discovered during the 1991 prospection, viz., Cochabamba (Río Seco), Santiváñez South (Aguada Loma) and Pajcha Pata (Fig. 3). Trace-fossils from this formation have been described by Rodrigo de Walker and Toro (1987) and Toro *et al.* (1990a).

Two other localities outside this area have recently been mentioned in Bolivia: the first one by Ramírez *et al.* (1992) in the vicinity of Teoponte, 115 km NNE of La Paz, in an unnamed Middle Ordovician sequence; the second one is recorded by Suárez Riglos (1993) near Sella, 20 km north of Tarija, southern Bolivia, from the Obispo Formation (Early Ordovician, i.e., Tremadoc-Arenig after Aceñolaza, Baldis *et al.*, 1987).

Finally, another fossiliferous site is reported in South America, that is in Argentina by Albanesi and Benedetto (1993) who mention ichthyoliths from the Upper Llanvirn of the La Cantera Formation of the San Juan Precordillera.

The fossiliferous locality of Argentina, shortly mentioned by Albanesi and Benedetto (1993), is fully described by Albanesi *et al.* (1995). It is located in the quebrada Don Braulio, on the eastern flank of the Sierra de Villicum, eastern San Juan Precordillera. The faunal assemblage comes from clasts of calcareous sandstones within the basal conglomerate of the La Cantera Formation. It is composed of fragmentary remains of *Sacabarnbaspis janvieri* and conodonts (*Eoplacognathus lindstroemi, Phragmodus flexuosus, Rhodesognathus* cf. *inaequalis, Panderodus* aff. *gracilis, Erismodus* n. sp. A, *Drepanoistodus* sp.), indicative of an early Llandeilo age after Albanesi *et al.* (1995).

Cochabamba. Very fragmentary vertebrate remains have been collected on Cerro San Pedro (Fig. 3D1) in the eastern suburb of Cochabamba (17°23'25" S. lat., 66°07'40" W. long.; Gagnier, 1991). They come from brownish detrital levels with *Bistramia elegans* and other unidentifiable brachiopod fragments. Few meters below, a green-yellowish fine-grained sandstone yielded *Dignomia bolivia* and *Bistramia elegans*.

Another site along the eastern outway of Cochabamba was mentioned in 1991 by Lic. Jorge Lobo of the Centro de Tecnología Petrolera (CTP) of YPFB at Santa Cruz de la Sierra. It is located about midway to Sacaba, north of Puntiti, in a creek locally named Río Seco (Fig. 3D2). A fragment of *Sacabambaspis* has been collected by J. Lobo in brown-yellowish fine-grained sandstones, intercalated with lingulid-bearing siltstones. Numerous coarser levels with trace fossils also occur. We could not find additional fish remains in 1991.

Sacabambilla. The best preserved *Sacabambaspis* specimens are from the Cerro Chakeri, Punata Province, north of Sacabamba (Gagnier, 1987, 1989), about 20 m below the old Cochabamba-Santa Cruz road, just before driving down to Sacabambilla which is located 50 km east of Cochabamba (17°30'00" S. lat., 66°47'58" W. long.; Fig. 3E). This section was measured in 1991 (Fig. 4A) from SE (northern flank of Cerro Cawara) to NW (southern flank of Cerro Chakeri), going down through the sequence. The mean dip is 25°N170.

The different fossil records since 1986 in this section are as follows:

- in the lower part of the section bivalves were collected in 1988 half way to the top of Cerro Chakeri in brown-yellowish sandstones with *Skolithos* bioturbation. They were identified by C. Babin as *Nuculoidea* sp., *Tancrediopsis?* sp., Ambonychiacea gen. indet. and Modiomorphidae? gen. indet. (Fig. 4A) [*Tancrediopsis* is classically known from the Middle-Upper Ordovician of N. America: Murray, 1985];
- the sample 91–11 yielded articulated specimens of *Sacabambaspis*; however, their state of preservation did not allow good histological thin sections to be made;
- above this level, the 1987 expedition had collected a large slab with numerous completely articulated specimens of *Sacabambaspis* and a concretion with a three-dimensionally preserved specimen (Gagnier, 1993). It corresponds to our sample 91–1 which also yielded numerous lingulids: *Dignomia bolivia* occurs within fine to coarser, 0.5–1 cm-thick, sandstone beds which contain exclusively flat-lying fragments of lingulid valves, with rarely more or less complete valves (Emig *et al.*, in press). Some complete, rather well-preserved, large valves have been collected within a coarse sandstone layer. Below and above the lingulid beds, many vertical cylindric burrows appear and might be interpreted as those of the lingulids;
- another site with *Sacabambaspis* was discovered in 1988–89 about 10 m higher in the section;
- finally, the trilobite *Homalonotus (Brongniartella) bistrami* has been collected at the level of the road.

Anzaldo. The type-locality of the Anzaldo Formation (Tarata Province, Cochabamba Department) has yielded in 1987 small fragments of *Sacabambaspis* in detrital beds with numerous inarticulate brachiopod remains. The outcrop is located in the cliff of the Río Anzaldo, leaving the village to Cochabamba (17°46'30" S. lat., 65°55'53" W. long.; Fig. 3 G). The ca. 2000m-thick type-section of the formation was described here by Rivas (1971). New fragmentary remains of *Sacabambaspis* were collected in 1991. The part of the sequence where they come from is mainly made of metric bedded green-yellowish sandstones with numerous trace fossils and sporadic phosphatic levels. Lingulids are rare, but a fragmentary undetermined nautiloid was collected (sample 91–13a; det. C. Babin). It probably corresponds to the upper

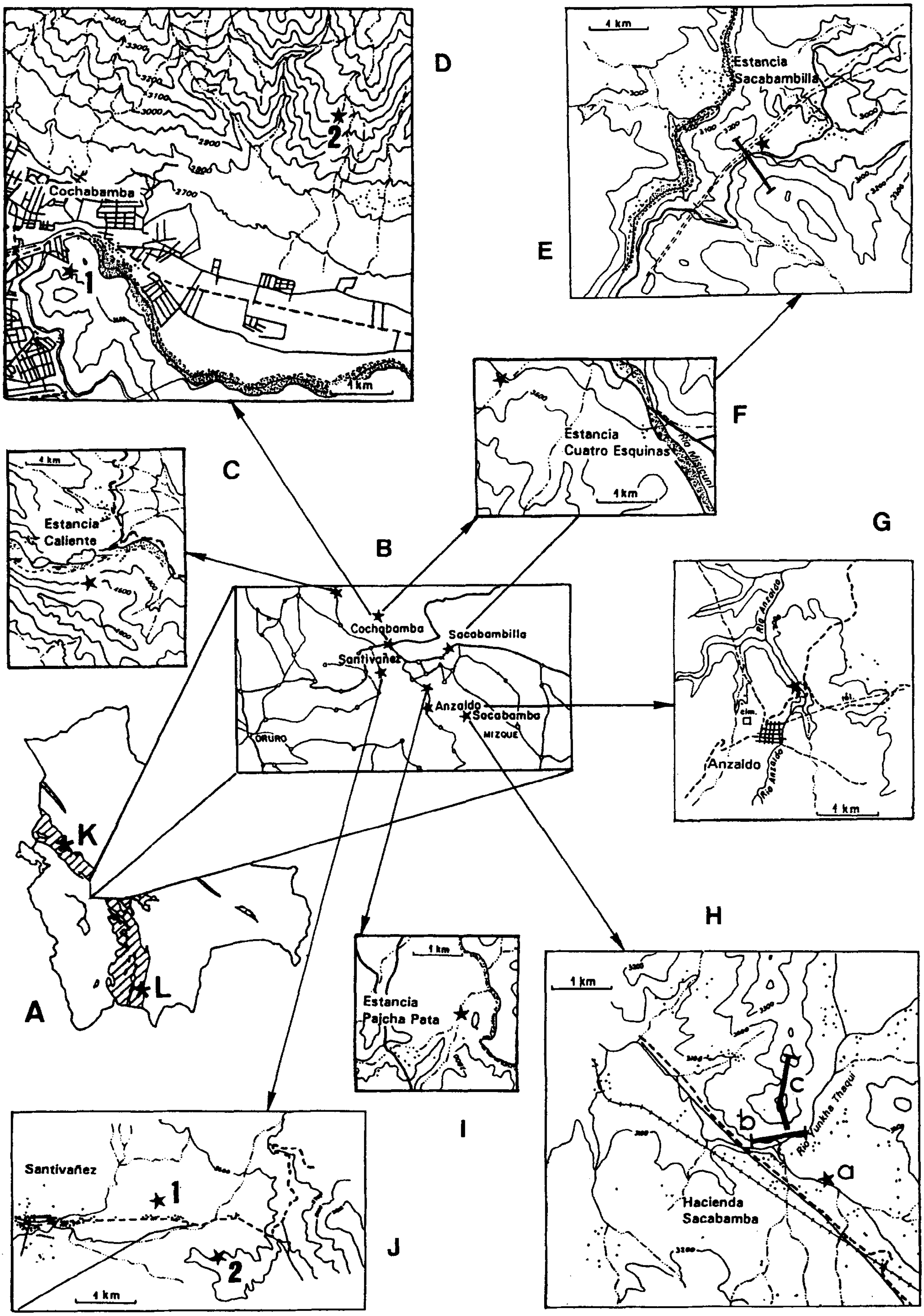

Fig. 3. The *Sacabambaspis* localities of Bolivia. A- location of the Ordovician outcrops (hatched); B- the localities in the Cochabamba region; C- Estancia Calientes (Cerro Lloja Pata Punta); D- east of Cochabamba: 1- Cerro San Pedro, 2- Río Seco; E- Estancia Sacabambilla (the fish locality and the measured section); F- Estancia Cuatro Esquinas (Río Millu Mayu); G- Anzaldo; H- Hacienda Sacabamba: a- the 1991 fish locality, b- the section measured in 1991, c- the section measured by Rodrigo (1986); I- Estancia Pajcha Pata; J- Santivañez: 1- North, 2- South (Aguada Loma); K- Teoponte; L- Sella.

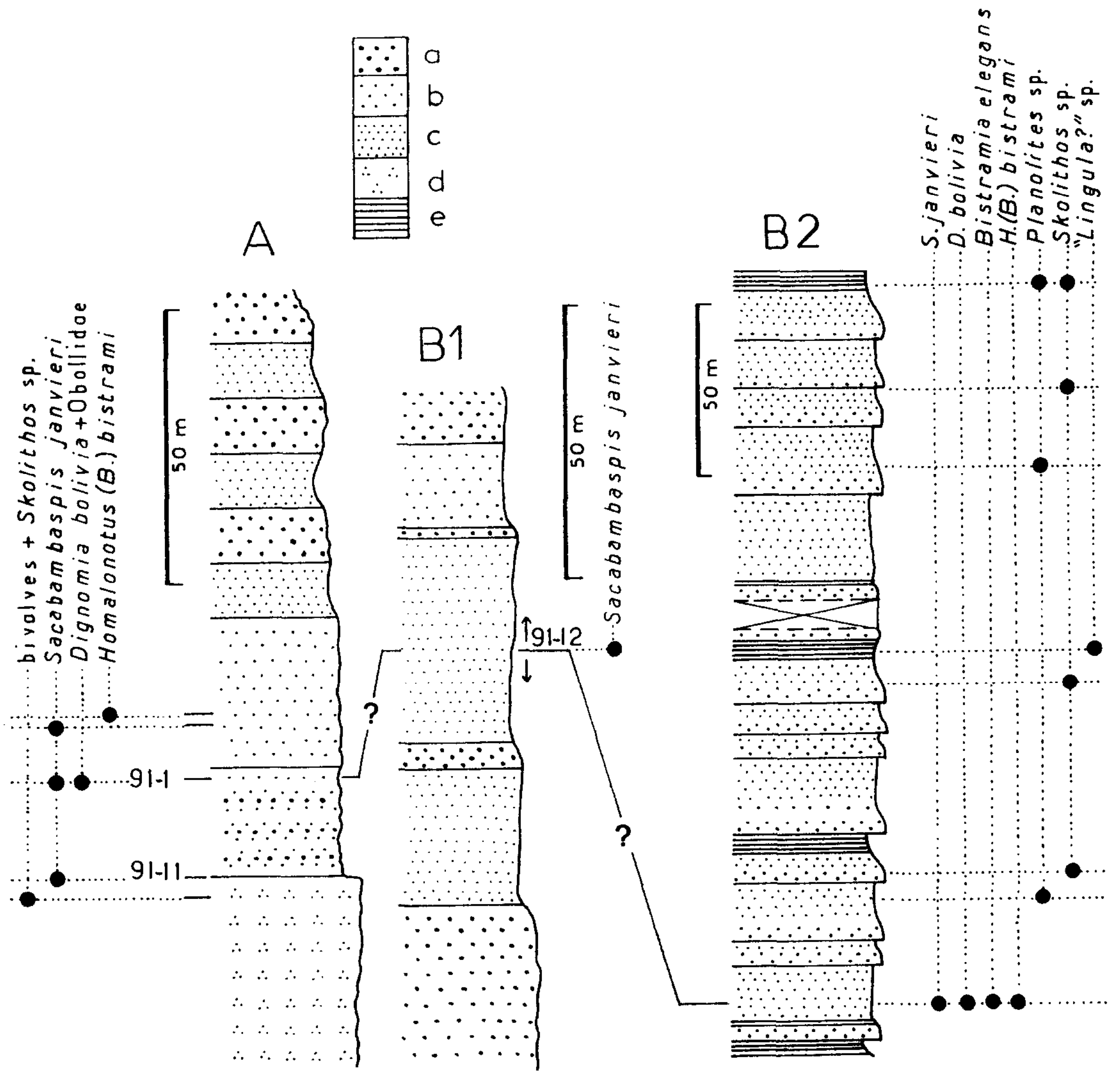

Fig. 4. Stratigraphical sections of two *Sacabambaspis* localities in the Anzaldo Formation. A- at Sacabambilla, measured in 1991 (E on Fig. 3); B- at Sacabamba: 1- measured in 1991 (Hb on Fig. 3), 2- measured by Rodrigo (1986; Hc on Fig. 3). a: coarser-grained sandstones, b: finer-grained, argillaceous/micaceous sandstones, c: bedded siltstones, d: massive siltstones, e: shales.

Anzaldo Formation, which underlies the quartzitic San Benito Formation.

Sacabamba. The type-locality of *Sacabambaspis janvieri* is Sacabamba, Department of Cochabamba, in the bed of Río Challaque, on the boundary between Mizque and Esteban Arze Provinces (Gagnier, 1987; Gagnier *et al.*, 1986). It is located 60 km south of Cochabamba (17°48'50"S , 65°47'08" W; Fig. 3H). Two new articulated *Sacabambaspis* specimens were found along the Río Challaque, south of its confluent with Río Yunkha Thaqui (Fig. 3 Ha; samples 91–12). The section was measured north of this point, along the northern edge of Río Challaque-Río Yunkha Thaqui, below the white quartzite which crops out on top of the cerro (Fig. 3Hb, 4B). It is composed of medium-grained to fine-grained sandstones and siltstones with numerous lingulid-bearing beds and trace fossils. This section seems to correspond to the middle part of the sequence described by Rodrigo de Walker and Toro (1987, Fig. 3), which is interpreted as a *Skolithos* ichnofacies. It has been correlated to the sections of Santiváñez and Cuchupunata (Rodrigo de Walker and Toro, 1987).

The original type-specimen of *Sacabambaspis* came from the base of a section logged towards the cerro by Rodrigo (1986). The fauna of the 3–4m thick vertebrate-bearing level is composed of *Bistramia elegans*, lingulids (originally attributed to *Lingula muensteri* and *L. ellipsiformis*) now attributed to *Dignomia bolivia*, and *Homalonotus* (*Brongniartella*) *bistrami*. Most of the brachiopod remains are ground but valves of *D. bolivia* occur. This part of the section is composed of lutites, well-bedded yellowish sandstones with a limonitic alteration, and grey to greenish grey and yellow sandstones. Poorly preserved chitinozoans (*Desmochitina* sp., *Conochitina* sp.), acritarchs (leiospheres, *Micrhystridium* sp., *Veryhachium* sp.) and conodonts were recovered from these beds (F. Paris, pers. comm. to PYG).

Pajcha Pata. This is a newly discovered fossiliferous site, along a creek named Quebrada Apacheta, northeast of Pajcha Pata (Fig. 3 I). The sequence is mainly composed of metric bedded sandstones of the Anzaldo type facies, alternating with grey siltstones with numerous big lingulid shells, as in Sacabamba. The sample 91–14 comes from this facies: it contains a patch of body scales and fragments of shields, the ornamentation of which clearly indicates *Sacabambaspis janvieri*. The whole section probably corresponds to the lower Anzaldo Formation (see Rivas, 1971). Some samples have also yielded bivalves (Bivalvia indet. and *Praenucula* sp.; det. C. Babin).

Santiváñez. Two fragmentary but well preserved specimens of *Sacabambaspis* were discovered in 1987 on a small hill, north of the eastern outway of Santiváñez, Cochabamba Department (Santiváñez North, 17°32'42" S, 66°12'12" W; Fig. 3J1). A new locality was discovered in 1991, south of it (Santiváñez South, Fig. 3J2), on the Aguada Loma hill. The section is here made of monotonous alternations of yellow fine-grained sandstones and more massive, quartzitic, whitish sandstones with cross-stratifications and pseudonodular beds. Several *Cruziana* as well as two *Sacabambaspis* specimens were found (sample 91–10). No lingulid occurs in this section which thus seems to correspond to the upper part of the sequence described by Rodrigo de Walker and Toro (1987, Fig. 4: *Cruziana* ichnofacies).

Cuatro Esquinas. Toro *et al.* (1990b) mention "un resto casi completo, al que le falta la región caudal" of *Sacabambaspis* in the Río Millu Mayu, section at Cuatro Esquinas, northwest of Cochabamba (Fig. 3F). It comes from the upper Anzaldo Formation, which also yields *Neonereites* trace fossils.

Calientes. Toro *et al.* (1990b) have found "pequeños fragmentos con ornamentación similar a los ilustrados por Gagnier (1986–1987)", in two levels of the upper Anzaldo Formation on the Cerro Lloja Pata Punta (Fig. 3C). It is particularly interesting to note that these fragments come from calcareous beds, in association to lingulids, conodonts and trilobites, in a sequence with abundant ichnofossils (*Cruziana*, *Planolites*, *Skolithos*). A pygidium of the trilobite *Homalonotus* (*Brongniartella*) *bistrami* is determined from this locality (Toro *et al.*, 1990b, Fig. 1). The conodonts which have been preliminary determined, would indicate a Middle Ordovician (Llanvirn-Llandeilo) age [M. Toro *et al.*, unpublished report, pers. comm. to PYG]. *Neocoleodus* is from the Middle Ordovician of N. America, *Plectodina* and *Phragmodus* from the Middle and Upper Ordovician of the USA and Europe, *Drepanoistodus* (*Oistodus*) being from the Ordovician of the Americas and Australia, but also from the Early Ordovician of Argentina (early Arenig).

Teoponte. A locality is mentioned by Ramírez *et al.* (1992) in the vicinity of Teoponte, Province of Larecaja, Department of La Paz (Fig. 3K), in the Río Kaka. A very distorted fragment of the posterior part of a dorsal shield with the adjoining squamation of *Sacabambaspis?* (P. Janvier, pers. comm., 1993) has been found in grey shales, in association to *Hoekaspis* sp., *Didymograptus* sp. and indeterminate brachiopods. These shales are considered of Llanvirn age by Ramírez *et al.* but are not formally attributed to any lithostratigraphic formation.

Sella. Suárez Riglos (1993) mentions ichthyoliths from the Obispo Formation of a section in the Tacsara anticline, at Sella, Méndez Province, Tarija Department. The formation yields the trilobite *Hoekaspis* as well as orthid brachiopods, *Orthoceras* and conodonts. It is dated as Early Ordovician (Tremadoc-Arenig *in* Aceñolaza, Baldis *et al.*, 1987). The microremains have been determined after schematic drawings sent to P. Janvier (pers. comm., 1993) as possible scales of thelodonts(?) or fragments of *Sacabambaspis*.

Tokochi, Cancañiri, and basal Kirusillas/Uncía formation

These units have been prospected in two different localities, one in the region of Cochabamba, one east of Lake Poopó (Fig. 5). The Cancañiri principally consists of glacial-marine diamictites and resediments. It is classically considered as equivalent to the Zapla Formation of

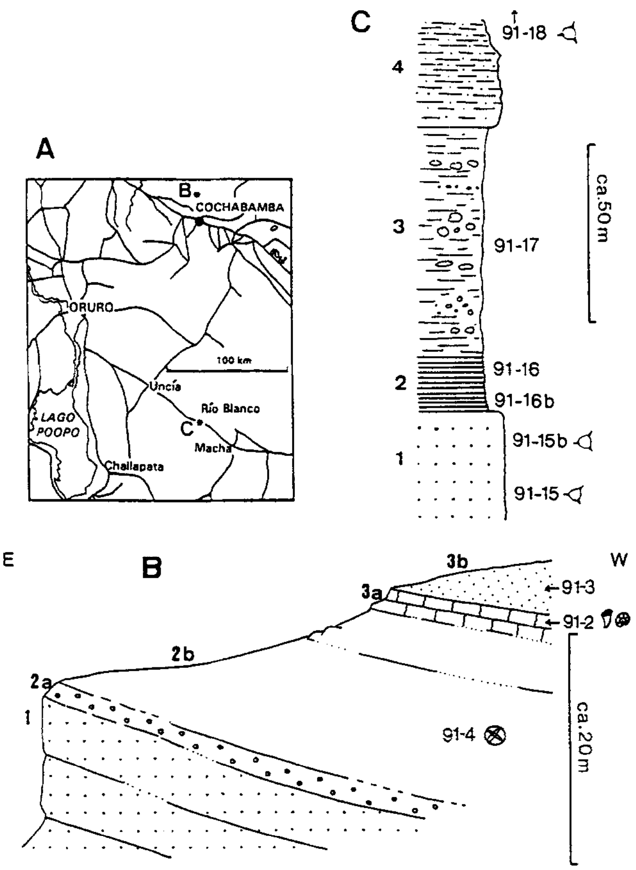

Fig. 5. Location and stratigraphical section of two sites of the Tokochi, Cancañiri and basal Kirusillas/Uncía Formations. A- geographical location; B- the section at Cuatro Esquinas: 1- quartzites of the San Benito Fm.; 2- Cancañiri Fm. with 2a- quartz-pebbled conglomerate, 2b- dark laminated siltstone; 3- Kirusillas/Uncía Fm. with 3a- Sacta limestone; 3b- sandstones with *Cruziana* and vertical burrows [with samples 91–2 to 91–4]; C- schematic log of the section at Río Blanco: 1- unnamed Ordovician dark sandstones and siltstones, 2- black shales (Tokochi Fm.), 3- dark siltstones and shales with sandstone and quartz pebbles (Cancañiri Fm.), 4- greenish and brownish sandstones (Huanuni member, Cancañiri Formation) [with samples 91–15 to 91–18].

northern Argentina, the top of which was dated as late Ashgill on the basis of trilobites (Monaldi and Boso, 1987). This age has been confirmed in Bolivia (Toro *et al.*, 1991, 1992).

Río Blanco (Tokochi and Cancañiri Formations). This section crops out well along the road from Oruro and Huanuni to Pocoata (Fig. 5), SE of Chuquihuati, in a long turn of the track. The Tokochi Formation overlies dark grey sandstones and siltstones of undifferentiated Ordovician age, and consists of several tens of meters of black shales. This unit is overlain by the Cancañiri Formation, which here consists of dark grey mudstones with sandstone and quartz pebbles (Fig.6C). Several samples come from this section:

- 91–15 and 91–15b in the underlying Ordovician sandstones;
- 91–16b in the Tokochi Formation;
- 91–17 in the Cancañiri Formation;
- 91–18 in overlying greenish and brownish soft silty sandstones assigned to the Huanuni member of the Cancañiri Formation.

Various microfossils (acritarchs, chitinozoans, scolecodonts) were prepared from 91–15, 91–15b and 91–18. Samples 91–16 and 91–17 only yielded dispersed organic matter with no microfossil.

Cuatro Esquinas (Cancañiri and basal Kirusillas/ Uncía Formations). The section is located west of Estancia Cuatro Esquinas, in a rather steep creek on the western side of the track along Río Titiri (17°11'21" S, 66°15'07" W). Above the Cuchupunata (=Anzaldo) Formation, the light-coloured quartzites of the San Benito Formation crop out as cliffs (Anaya *et al.*, 1987, figs. 1–2). They are overlain by the dark Cancañiri Formation, which begins with a 1 m-thick conglomeratic level with small quartzitic pebbles (Fig. 5), and is in turn overlain by a thin limestone unit at the base of the Kirusillas Formation.

Three samples have been taken:

- 91–4 in the massive, dark, argillaceous siltstones of the Cancañiri Formation which yielded abundant acritarchs (see below);
- 91–2 in the 1m-thick carbonate fossiliferous bed at the base of the Kirusillas Formation (Sacta limestone member, as documented below).
- 91–3 in silty sandstones of the lower Kirusillas (= Uncía) Formation, with *Cruziana* and vertical burrows.

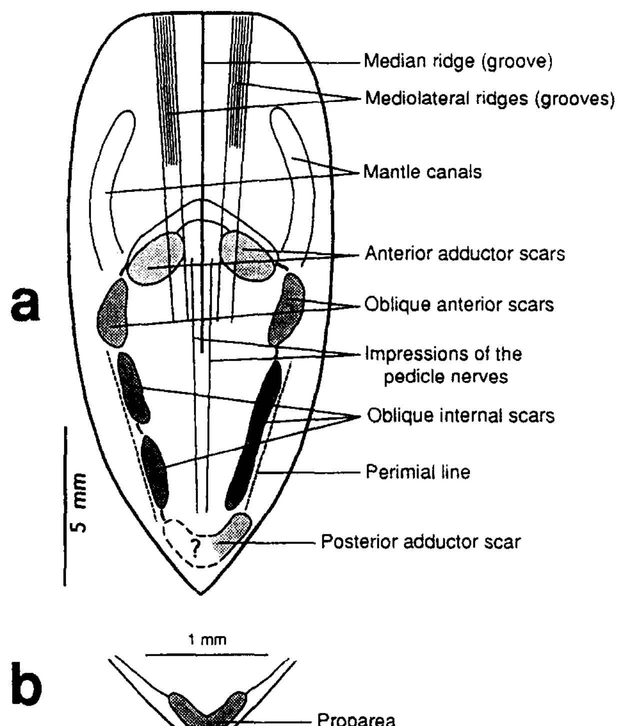

Fig. 6. *Dignomia boliviana*. a- internal mould of a ventral valve with internal morphology (arrangement of the musculature and disposition of the two main anterior mantle canals). The pair of V-shaped narrow grooves extending posteriorly from the anterior adductor scars correspond to the impression of the pedicle nerves; b- umbonal region of the internal side of a ventral valve.

BIOSTRATIGRAPHICAL RESULTS

Brachiopods (CCE)

The recently described lingulid genus *Dignomia* Emig *et al.* (in press) has been collected in the Anzaldo Formation. Its stratigraphical range is from the Late Ordovician to Middle Devonian and its presently known geographical distribution is restricted to North and South America (Emig *et al.*, in press). *Dignomia*, as almost lingulid genera, cannot in general be used as a chronostratigraphic fossil.

Acritarchs (MV)

In the following, the sign (°) corresponds to single or few specimens of prepared microfossils, and the sign (°°) to several to numerous specimens observed.

Río Blanco section. *Samples 91–15 and 91–15 b*: presence of broken undetermined chitinozoans and scolecodonts; mainly polygonomorphid, moderately abundant acritarchs: *Villosacapsula? rosendae -helenae* (Cramer) Loeblich and Tappan, 1976 (°°), *Veryhachium*? sp. (smooth triangular forms with broken processes) (°), *Veryhachium europaeum* Stockmans and Willière, 1960 (°) [Pl. 2: 4–6].

Villosacapsula rosendae and *V. helenae* first appear in Late Ordovician strata. They are both cited in Bohemia (Vavrdova, 1974) and the former one in France (Rauscher, 1974). Both species are also known in younger strata. *Veryhachium europaeum* has a similar range. It appears in Late Ordovician strata (Martin, 1969). Those species are not at all demonstrative for a precise age. In absence of Silurian species, a Late Ordovician age is however suggested. The assemblage is quite different from some other Early and Middle Ordovician assemblages recovered in scattered samples in southern America (Bultynck and Martin, 1982; Ottone *et al.*,1992; Volkheimer *et al.*,1980; Théry *et al.*,1986).

Sample 91–18 : very rich and diversified assemblage containing mainly acritarchs and poorly preserved undetermined chitinozoans. The following species have been identified:

Actinotodissus cf. *A. crassus* Loeblich and Tappan,1978 (°) [Pl. 2: 11]
Arkonia cf. *A. tenuata* Burmann, 1970 (°) [Pl. 2: 13]
Diexallophasis ? sp. A (°) [Pl. 2: 12]
Diexallophasis remota (Deunff) Playford, 1977 (°) [Pl. 2: 3]
Moyeria? cabottii (Cramer) Miller and Eames, 1982(°)
Multiplicisphaeridium raspum (Cramer) Eisenack *et al.*, 1973 (°)
Neoveryhachium carminae (Cramer) Cramer, 1970 (°°) [Pl. 2: 7–8]
Striatotheca principalis parva Burmann, 1970 (°) [Pl. 2: 10]
Tylotopalla sp. (°)
Villosacapsula? setosapellicula (Loeblich) Loeblich and Tappan, 1976 (°°) [Pl. 2: 1–2].
The assemblage comprises also several undetermined netromorphid specimens (°°).

Arkonia tenuata, Striatotheca principalis parva, Actinotodissus crassus and *Villosacapsula setosapellicula* are Ordovician species, Early to Middle Ordovician for the former two (see for instance Burmann, 1970), Late Ordovician for the two last ones (see for example Molyneux, 1988). *Diexallophasis remota, Moyeria cabottii* and *Tylotopalla* sp. are ubiquitous in Late Ordovician and Silurian strata (Martin, 1988, 1989). *Neoveryhachium carminae* is commonly found in the Silurian (for example in the Ludlovian of Cochabamba in the Eastern Andes of Bolivia, Cramer *et al.*,1974a). However Ordovician specimens are recorded under different names by Cramer *et al.* (1974b, as *N. carminae*), Rauscher (1974, as *V. carminae*), Loeblich (1970, as *V. carminae*) and Molyneux (1988, as *Neoveryhachium* sp. A). By one feature (the processes length), the Bolivian specimens do conform with the Late Ordovician Libyan material (Molyneux, 1988) rather than generally reported Silurian specimens of *N. carminae*. Thus the present data point better to a Late Ordovician age than to the Silurian.

Cuatro Esquinas section. *Sample 91–4* : very abundant sphaeromorph acritarchs (°°); rare *Gorgonisphaeridium* (°) and/or *Micrhystridium* (°); probable presence of *Veryhachium* (°), represented by smooth, triangular and quadrangular forms with broken processes.

The latter specimens agree with an Ashgill age admitted for the lower part of the Cancañiri Formation. However they do not demonstrate that age. The predominance of sphaeromorphs suggests a nearshore environment. Benedetto *et al.* (1992, p. 123) have reported a so-called "*Helios aranaides-Duvernaysphaera gothica*" association characterising the Cancañiri Formation, but they did not cite the origin of this information. No trace of it has been found in the published available literature. As it is presented by Benedetto *et al.*, it seems that we are in the presence of two distinct species. In fact, only one species is here concerned as Cramer and Diez (1972) have maintained only one taxon: *Duvernaysphaera aranaides* (Cramer,1964). They indeed consider *Helios* as a junior synonym of *Duvernaysphaera*, and *gothica* as a junior synonym of *aranaides* (for more details see Fensome *et al.*, 1990). This species of Silurian affinity (Le Hérissé, 1989) has not been recorded in our studied sample.

Calcareous microfossils (DV)

These fossils were sampled in the limestone overlying the Cancañiri Formation at Cuatro Esquinas. Two types of microfacies have been observed in this limestone: (1) micritic and sparitic, trilobite-bearing wackestones (thin sections 91–2A, C and F; Pl. 1: 2–4), and (2) nodular silty wackestones/packstones with ostracodes (thin sections 91–2B and D-E; Pl. 1: 5). The first type contains common or very common shells of trilobites, with relatively common ostracodes, rare pelmatozoans, rare brachiopods, and various very rare groups: bryozoans, favositid corals (Pl. 1: 1), calcitized hexactinellid sponge spicules, phosphatic fragments and Foraminifera. The second type contains very common ostracodes with relatively common trilobites, rare pelmatozoans, rare brachiopods, and very rare bryozoans, phyllotriaene spicules, phosphatic fragments and Foraminifera. The foraminiferal assemblage contains *Psammosphaera* sp., *Webbinelloidea?* sp., *Parathurammina?* or *Thurammina* auct., *Lagenammina* sp., *Hyperammina?* sp. as well as two indeterminate taxa with foraminiferal or reitlingerellid affinities, and is suggestive of a Silurian (Wenlock) age. It is from this limestone that Anaya *et al.* (1987) figure the cystiphyllid rugose coral *Dalmanophyllum*, of "Lower and Middle" Silurian age, i.e., Llandovery-Wenlock.

The foraminiferal assemblage from the base of the Kirusillas/Uncía Formation at Cuatro Esquinas is relatively similar to the Silurian microfauna of the Arbuckle Mountains of Oklahoma, USA, previously described by Moreman (1930, 1933), Ireland (1939) and Amsden *et al.* (1980). The same age is tentatively proposed for the Bolivian assemblage, i.e., Wenlock. General data for North American Foraminifera by Conkin and Conkin (1985) agree with this Silurian age. This limestone is thus a lateral equivalent of the Sacta limestone member of the lower Kirusillas (=Uncía) Formation known in the area located 180–200 km east of Cochabamba. The Sacta limestone has yielded Sheinwoodian (early Wenlock) conodonts in the Sacta section and in the Ichoa well (Merino Rodo, 1991, and pers. comm.).

SYSTEMATIC PALEONTOLOGY

AcritarchA (MV)

Actinotodissus cf. *A. crassus* Loeblich and Tappan, 1978: on the few specimens encountered, the median ribs of the holotype are lacking, as they are on the specimens described and figured by Molyneux (1988) in the Late

Ordovician from northeast Libya. The dimensions of the figured specimen (Pl.2: 11) are as follows: vesicle diameter 28 mm; process length up to 20 mm; number of processes at each pole ≈12.

Arkonia cf. *A. tenuata* Burmann, 1970: nine rather fine ribs are numbered from the border to the center of the shell (Pl. 2: 13). The holotype bears 10–12 ribs. The processes are much shorter than the ones of *Arkonia virgata* Burmann, 1970. The shell of the latter species has ≈ 7 ribs.

Diexallophasis? sp. A is a multifurcated acanthomorph with very fine ribs but without spines on the stems of the process. The shell is unfortunately deformed, presumably by pyrite formation. Its ornamentation is therefore hidden (Pl. 2: 12).

Neoveryhachium carminae (Cramer) Cramer, 1970: some specimens (Pl.2: 7) are very well showing the external veil typical for the genus. In some others (Pl.2: 8), this veil is absent. The specimen of Pl.2: 9 has more ridges than the holotype of the species. All encountered specimens have relatively short processes. Their length is more or less equal to the length of the shell. The specimen of Pl.2: 8 has a process length of 16 and 19mm and a diameter of the shell of 17mm.

Striatotheca principalis parva Burmann, 1970: the dimensions of the figured specimen (Pl. 2: 10) are as follows: vesicle diameter 26 mm; process length 18 mm; 6 ribs from the border to the center of the central body.

Villosacapsula? rosendae-helenae (Cramer) Loeblich and Tappan, 1976: both species are here combined in a single complex as we have been unable to discriminate *rosendae*, with arched sides from *helenae*, with staight sides of the shell. The ornamentation of conical appearence does not correspond exactly to the original definition of the species. This is perhaps due to the poor preservation of the specimens (Pl. 2: 4–6).

Villosacapsula? setosapellicula (Loeblich) Loeblich and Tappan, 1976 has a very pronounced (Pl.2: 1) or softer (Pl.2: 2) ornamentation of the shell, ranging from ≈1/3µm to ≈3/4µm in diameter. These ornaments have a conical profile, not typically the spine-like aspect of the holotype. This could be due to the preservation. The length of the processes conforms the length of the ones of the type material. *Villosacapsula irrorata* (Loeblich and Tappan) Fensome *et al.*, 1990 has much longer processes.

Foraminifera (DV)

The foraminiferal assemblage shows the following composition. Each taxon is exceptionnally present.

- *Psammosphaera* sp. (91–2F, 2C)
- *Webbinelloidea* (?) sp. (91–2A)
- *Parathurammina* (?) or *Thurammina* auct. (91–2C)
- *Lagenammina* sp. (91–2C, 2D)
- *Hyperammina* (?) sp. (91–2A)
- gen. indet. 1 (91–2C, 2F)
- gen. indet. 2 (91–2A).

The two last taxa are problematic and exhibit affinities with the Foraminifera (*"Glomospira"*; *"Tolypammina"*) or the Reitlingerellids.

Brachiopoda (CCE)

Class Inarticulata Huxley, 1869
Order Lingulida Waagen, 1885
Superfamily Lingulacea Menke, 1828
Family uncertain
Genus *Dignomia* Hall, 1871
Dignomia bolivia Emig *et al.*, in press

Preliminary remark: Two species, described from the same area and classically identified (Súarez Soruco, 1976) as *Lingula muensteri* and *L. lineata*, are probably synomyms of *Dignomia bolivia*. Some of the taxonomic characters indicated herein have been recently analyzed in an anatomical study of Mesozoic lingulids by Biernat and Emig (1993) who argue that no Palaeozoic or Mesozoic genus of Lingulidae belongs to the extant genera *Lingula* and *Glottidia*.

Description (Fig. 6): Elongate oval outline of the shell with two large, longitudinally striated, medio-lateral grooves, and a narrow median groove, all three extending from the anterior margin to about the two thirds of the shell length on the ventral valve and to the umbonal region on the dorsal valve. Anterior margin, generally straight, with indentation at the level of the grooves. Lateral margins subparallel. Biggest width between the middle and the anterior third of the length of the shell. External surface smooth with numerous weak, sometimes well-marked, growth lines. Umbonal region rounded on the dorsal valve, pointed on the ventral valve. Small proparea lightly curved with a weak pedicle groove, continuous to the internal valve face. Internal characters weakly visible on one ventral mould: extension of the ventral lophophoral cavity to approximately 36% of the valve length; ventral mantle canals curved; one pair of narrow subparallel, V-shaped, grooves extending from the anterior adductor scars to the posterior adductor; large oblique muscle scars, and a V-shaped perimial line. The length of the shells varies from 12 to 30mm (mean 19.1mm; n=12), the width from 5.9 to 14mm (mean 9.3mm), and the ratio W/L from 0.45 to 0.55 (mean 0.49).

Vertebrata (PYG & AB)

Class Pteraspidomorphi *sensu* Gagnier, 1991
Order Arandaspidiformes Ritchie and Gilbert-Tomlinson, 1977
Family Arandaspididae Ritchie and Gilbert-Tomlinson, 1977
Genus *Sacabambaspis* Gagnier, Blieck and Rodrigo, 1986
Sacabambaspis janvieri Gagnier, Blieck and Rodrigo, 1986

Most of the specimens collected in 1991 are fragmentary. *Sacabambaspis* has been shortly described in preliminary papers (Gagnier *et al.*, 1986; Gagnier, 1987, 1989, 1991; Blieck *et al.*, 1991; Elliott *et al.*, 1991; Gagnier and Blieck, 1992) and is fully detailed by Gagnier (1993).

Two specimens only from Sacabambilla bear interesting features. The first one has a tail without any chordal extension contrary to what was originally thought by Gagnier (1989). This point was strongly discussed and the caudal paddle is redescribed by Gagnier (1993) as being symmetrical with equal or subequal dorsal and ventral scale-covered webs. The second specimen shows a mouth part covered of minute scales in a fan-shape structure which recalls the heterostracan one.

ENVIRONMENTAL AND PALEOGEOGRAPHICAL REMARKS

Anzaldo Formation (CCE)

Within the named "Lingulid sandstone" (*sensu* Steinmann and Hoek, 1912) of the Anzaldo Formation, the *Dignomia* have been fossilised under several beds of numerous flat-lying valves, but rare *in situ* shells occur. The lingulid-bearing sandstone layers are separated from each other by 3–4 to 20cm thick argillaceous sandstone levels. In the light of recent ecological investigations on living *Lingula* (Emig, 1986), the fossilisation of flat-lying valves is the consequence of a drastic environmental change (viz., salinity decrease, storm effect, very fine or coarse sedimentation). The absence of fossil *Dignomia* shells in other sandstone layers does not preclude the absence of *Dignomia* populations because the shell of the lingulids is not preserved in normal life conditions (Emig, 1990). Various interpretations of the *Dignomia* fossilisation may be proposed; it can indeed be the consequence of:

— strong storm effects: the sediment is dismantled, and the lingulids (mainly crushed *Dignomia* valves) awashed and accumulated on the shore line, that would also explain the occurrence of the phosphorite levels ;

— low salinity waters (less than 15% over at least 2–3 days), due to exceptional rains and/or river swellings, generally with fine or coarse sedimentation leading to valve fossilisation. Such conditions, consistent with the presence of some *in situ* shells of *Dignomia*, occur in the intertidal zone near a river estuary or delta, about every 4 years according to the shell size (transposed from observations on living *Lingula* populations). Furthermore, the sediment in which the *Dignomia* have been fossilised appears close to the substrate in which they normally live (Emig, 1984).

Cancañiri formation (MV)

Amongst the two samples collected in the Cancañiri Formation, sample 91–4 from the Cuatro Esquinas exposure yields abundant microfossils, namely profuse sphaeromorphs and a few polygonomorphid acritarchs. The sample 91–17 from Río Blanco shows unidentifiable fragments of organic matter. It is devoid of figured specimens of acritarchs or anything else. The occurrence of acritarchs in the lower part of the Cancañiri Formation is interesting with respect to the glacial conditions reportedly prevailing during the deposition of this formation. Indeed, acritarchs are largely accepted as indicating marine conditions. Therefore, the sediments here involved have a glacial marine origin. This conclusion has already been obtained by Laubacher *et al.* (1982, p.1168) who found acritarchs and possibly chitinozoans and scolecodonts in the Zapla Shale at Pojo, a Bolivian locality somewhat 150 km east of the studied area. They also recorded acritarchs and chitinozoans within the Cancañiri Formation (Laubacher *et al.*, 1982, locality B-2, table 12, p. 1144). Laubacher *et al.* did not detail the type of acritarchs they recorded. In the Cuatro Esquinas section, the assemblage is at nearly 100% composed of simple sphaeromorphs. This type of assemblage is often interpreted as an indicator of a shallow marine environment. Tongiorgi and Ribecai (1990) have observed a sphaeromorph dominated assemblage near the Cambrian-Ordovician boundary at Öland (Sweden). They connected this observation to regressive events (Erdtmann ARE plus PRE) which are in turn related to eustatic lows of glacial origin. Thus, if this interpretation is correct, the abundance of sphaeromorphs as recorded in the Bolivian Cancañiri Formation agrees well with the glacial-marine facies of the host sediment.

Sacta limestone member of the basal Kirusillas/Uncía Formation (DV)

The limestone at the base of the Kirusillas/Uncía Formation at Cuatro Esquinas was deposited in an outer platform, in the vicinity of an area of important carbonate productivity. This suggests a warm subtropical climate. The very rare favositids collected in the samples probably indicate reworkings from a carbonate build-up.

Concerning the South American Silurian biogeographical location, the calcareous microfaunas did probably belong to the "warm-water North Silurian Realm" *sensu* Laubacher *et al.* (1982). They were markedly different from the "cool-water Malvino-Kaffric faunas".

CONCLUSIONS

The main aim of the 1991 expedition to Bolivia was to date the vertebrate-bearing Anzaldo Formation. For that, we tried to find fossiliferous sites within the Anzaldo Formation itself but also in the underlying and overlying formations. Our results are summarized hereafter.

The supposed "Capinota" Formation of the Iglesiani valley did not reveal any additional vertebrate. On the contrary, it proved to be in fact of Devonian age, and thus to have been erroneously assigned to this unit, which classically underlies the Anzaldo Formation, due to facies convergence (Blieck *et al.*, in press). These sites are thus of no help for the Ordovician vertebrate issue.

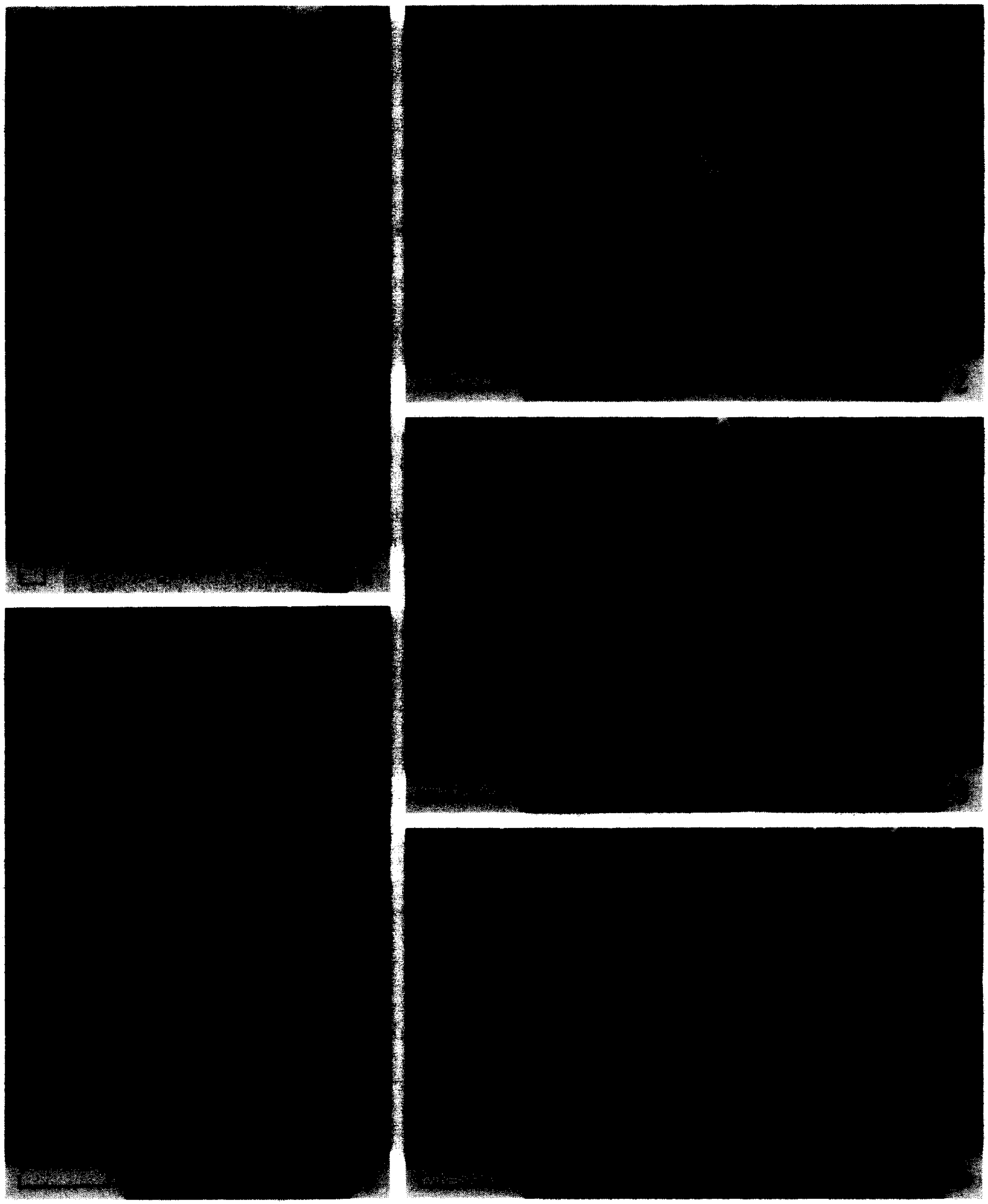

Plate 1. Microfacies of sample 91–2, Cuatro Esquinas section, Sacta limestone, Bolivia (collections of the Laboratoire de Paléobotanique, Sciences de la Terre, Université des Sciences et Technologies de Lille, France). Each black scale-bar equals 1mm. 1. Favositid colony abraded and surrounded by the transport. Sample 91–2. x3,5. 2. Bioclastic limestone with bryozoan (1) and trilobite (2). Slide 91–2F/6604. x15. 3. Micritic and sparitic wackestone with trilobites of various genera (1) and crinoids (2). Slide 91–2A/6593. x15. 4. Bioclastic limestone with trilobite (1), crinoid (2) and a rather big remain of a favositid coral (3). Slide 91–2C/6599. x15. 5. Silty nodular wackestone/packstone with very common disarticulated valves of ostracodes. Slide 91–2B/6597. x15.

The Anzaldo Formation yielded several localities with vertebrates but also with lingulid brachiopods and bivalves. The latter are poorly preserved and of no chronologic help. The former, attributed to *Dignomia bolivia* Emig *et al.*, are no longer a good stratigraphical index since they range from Late Ordovician to Middle Devonian times. Because the Anzaldo may be several thousands of meters thick, it probably encompasses some substantial period of time.

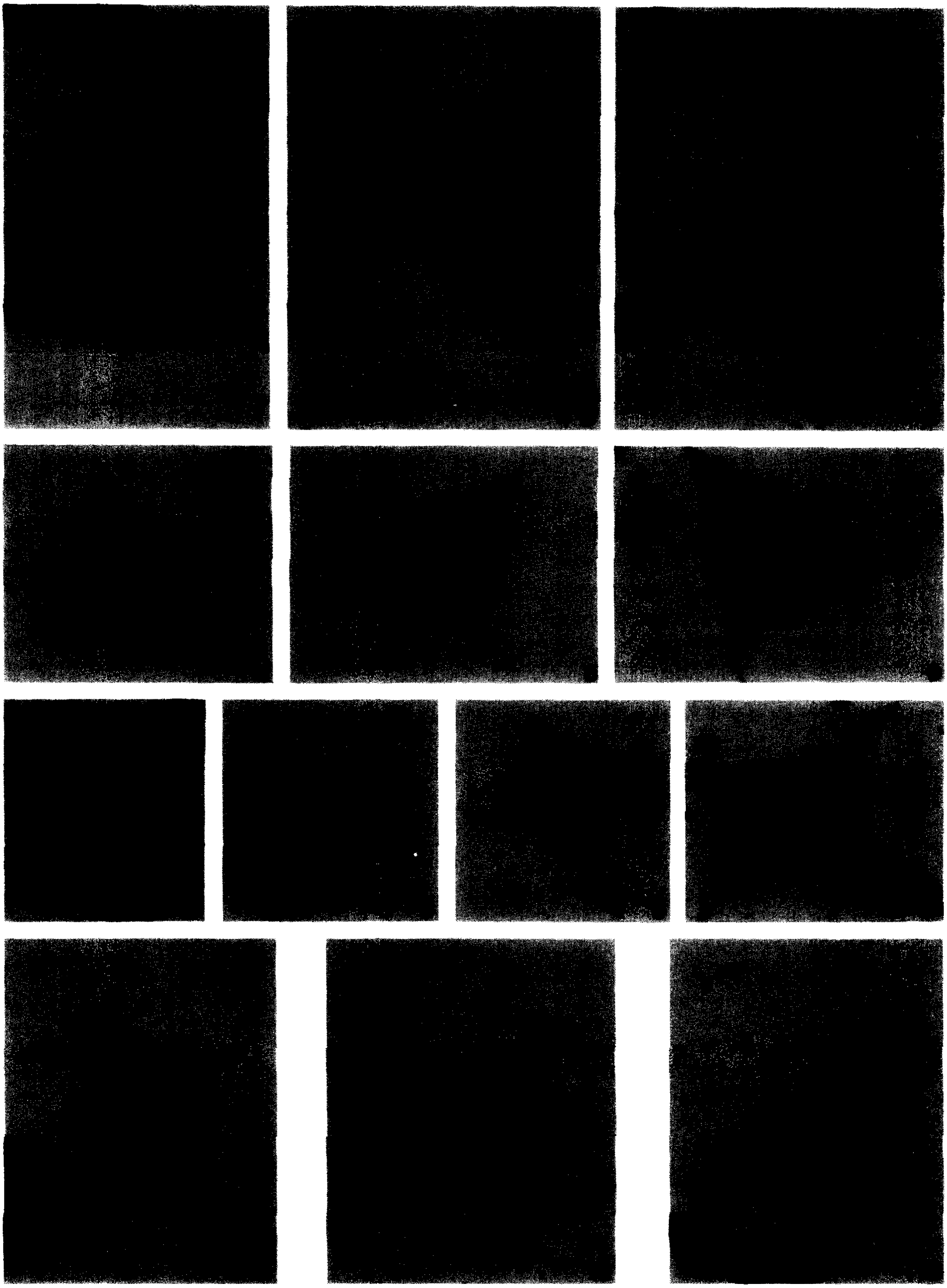

Plate 2. Acritarchs of the Río Blanco section (sandstones below the Tokochi Formation: sample 91–15; Huanuni member, Cancañiri Formation: sample 91–18), Bolivia (collections of the Laboratory of Palynology, Liége University, Belgium). All specimens at x1000. 1–2. *Villosacapsula? setosapellicula* (Loeblich) Loeblich and Tappan, 1976. 1: 91–18, 23010, T43/1–3; 2: 91–18, 23010, W38/4. 3. *Diexallophasis remota* (Deunff) Playford, 1977. 91–18, 22995, X43/3. 4–6. *Villosacapsula? rosendae-helenae* (Cramer) Loeblich and Tappan, 1976. 4: 91–15, 22991, K44/4; 5: 91–15, 22991, T40/1; 6: 91–15, 22991, F46/1. 7–8. *Neoveryhachium carminae* (Cramer) Cramer and Diez, 1970. 7: 91–18, 22995, R44/1–3; 8: 91–18, 22995, M36/1–2. 9. *Neoveryhachium?* sp. 91–18, 23010, Q34/2. 10. *Striatotheca principalis parva* Burmann, 1970. 91–18, 22995, W50/1–2. 11. *Actinotodissus* cf. *A. crassus* Loeblich and Tappan, 1978. 91–18, 22995, J53. 12. *Diexallophasis?* sp. A. 91–18, 22995, X53. 13. *Arkonia* cf. *A. tenuata* Burmann, 1970. 91–18, 22995, O53.

The mainly quartzitic San Benito Formation is several hundreds of meters thick, and is stratigraphically located between the Anzaldo and the Tokochi-Cancañiri Formations. It clearly shows a vertical, and thus lateral, transition with the Anzaldo Formation. It has not been precisely prospected mainly because it is composed of reputedly azoic quartzites forming high cliffs in the visited area. Thus the age of the Anzaldo Formation can be constrained only after data from the overlying Tokochi and Cancañiri Formations.

The acritarchs of samples 91–15 and 91–15b of the Río Blanco section, from sandstones underlying the Tokochi Formation, suggest a Late Ordovician age. Given their stratigraphic position just below the Tokochi sea-level high, these sandstones are probably coeval with the upper San Benito Formation of the Cochabamba area.

Fossils known from the Tokochi Formation suggest a Caradoc age.

The acritarchs of sample 91–4 at Cuatro Esquinas, from the Cancañiri Formation, have no precise stratigraphical meaning; they agree with an Ashgill age for this unit, proposed on other evidence in the literature.

The acritarchs of sample 91–18 of the Río Blanco section (Huanuni member, Cancañiri Formation) point rather to a Late Ordovician than to a Silurian age, in agreement with the Ashgill age assigned to this formation. Because the Cancañiri consists of resediments, the possibility exists that the organic microfossils of 91–18 are reworked.

The carbonate microfossils of sample 91–2 from the Cuatro Esquinas section, at the base of the Kirusillas/Uncía Formation, are suggestive of a Wenlock age, which matches the early Wenlock age demonstrated for the Sacta limestone member of the basal Kirusillas/Uncía Formation from 200 km more to the east. Stratigraphic and sedimentologic characteristics of this horizon in the whole basin strongly suggest that it marks the onset of a major transgression (see Fig. 2).

In addition, our data strongly suggest that a depositional and/or, more probably, erosional hiatus separates the Cancañiri Formation from the Sacta limestone member of the basal Kirusillas/Uncía Formation in the Cochabamba area. The previous studies and this work agree in that the Ordovician/Silurian boundary would lie somewhere between the upper part of the Cancañiri Formation, which has yielded a late Ashgill fauna, and the basal part of the Kirusillas/Uncía Formation, from which late Llandovery?-early Wenlock faunas are known. The Llallagua Formation, which is located between these two units in the more subsident part of the basin, consists of sand turbidites and has not yielded any diagnostic fossil yet.

From our data, the *Sacabambaspis*-bearing Anzaldo Formation cannot be more precisely dated than pre-Ashgill, i.e., Caradoc or older. However, previous paleontological studies do suggest that the age of this thick stratigraphic unit would span a probably substantial part of the Llanvirn-Caradoc time interval.

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NOTE ADDED IN PROOF

The fossiliferous locality of Argentina, shortly mentioned by Albanesi & Benedetto (1993), is fully described by Albanesi *et al.* (1995). It is located in the quebrada Don Braulio, on the eastern flank of the Sierra de Villicum, eastern San Juan Precordillera. The faunal assemblage comes from clasts of calcareous sandstones within the basal conglomerate of the La Cantera Formation. It is composed of fragmentary remains of *Sacabambaspis janvieri* and conodonts (*Eoplacognathus lindstroemi, Phragmodus flexuosus, Rhodesognathus* cf. *inaequalis, Panderodus* aff. *gracilis, Erismodus* n. sp. A, *Drepanoistodus* sp.), indicative of an early Llandeilo age after Albanesi *et al.* (1995).

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