Biostratigraphic precision of the *Cruziana rugosa* group: a study from the Ordovician succession of southern and central Bolivia

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Abstract – *Cruziana* ichnospecies have been repeatedly reported to have biostratigraphic significance. This study presents a re-evaluation of the arthropod ichnotaxa of the *Cruziana rugosa* Group from bio- and/or lithostratigraphically well-defined Lower to Upper Ordovician siliciclastic sections of southern and central Bolivia. With the exception of *Cruziana rouaulti*, the ichnofaunas contain all the members of the *Cruziana rugosa* Group throughout the Ordovician (Arenig to Caradoc) successions in Bolivia. The Bolivian material therefore indicates that these arthropod ichnofossil assemblages are suitable for recognizing Ordovician strata in Bolivia. These findings cast doubt on their use as reliable indicators for a global intra-Ordovician (Arenig to Caradoc) biozonation of Peri-Gondwanan sedimentary successions.

Keywords: *Cruziana*, biostratigraphy, Bolivia, Ordovician.

1. Introduction

The ichnotaxon *Cruziana* is one of the best-known arthropod ichnogenera used for facies analysis (Frey & Pemberton, 1984; Pemberton *et al.* 1992), but its biostratigraphic relevance is even more important because it enables dating of sandstone units lacking body fossils (Crimes, 1968, 1969; Seilacher, 1970, 1992, 1994). This approach has also served to subdivide Silurian oil-bearing units in Libya (Seilacher, 1992). Although some studies cast doubt on the biostratigraphic relevance of certain *Cruziana* ichnospecies (Magwood & Pemberton, 1990), the lack of indicative fossils accompanying *Cruziana* has prevented an independent control to date.

One of the most abundant *Cruziana* ichnoassemblages in the world is the '*Cruziana rugosa* Group'. It consists of the four members of *Cruziana furcifera*, *Cruziana goldfussi*, *Cruziana rouaulti* and *Cruziana rugosa*. Two members of this ichnoassemblage, *Cruziana furcifera* and *Cruziana rugosa*, were first described from the Ordovician successions of Bolivia (d'Orbigny, 1839, 1842). Stratigraphically, the '*Cruziana rugosa* Group' is restricted to Lower Ordovician strata according to Seilacher (1970, 1992), keeping in mind that Seilacher (1970, 1992) only subdivides the Ordovician into Lower and Upper without a Middle Ordovician interval, in contrast

to the present study. However, Bolivia is the only place worldwide where Seilacher (1992) reports that the occurrence of the '*Cruziana rugosa* Group' continues stratigraphically into the Upper Ordovician. Although Seilacher reassigned these Caradocian quartzites in Bolivia to the Middle Ordovician in a personal communication in Mángano & Buatois, 2003, the thick quartzitic units near Cochabamba are at least partly Caradoc in age (Gagnier *et al.* 1996). If this were true, Bolivia would offer the unique possibility to find out about the real stratigraphic range of the '*Cruziana rugosa* Group'. However, the presence of this ichnoassemblage in Upper Ordovician rocks as reported by Seilacher (1992) was not sustained by any independent biostratigraphic data. The present contribution therefore aims at dating these Upper Ordovician *Cruziana* occurrences with new fossil findings. Furthermore, in a later paper, Seilacher (1994, p. 754, fig. 2) returned to his earlier view with *Cruziana rugosa* being indicative only for the Lower Ordovician and did not discuss his own observations from Bolivia. The exact stratigraphic range of the '*Cruziana rugosa* Group' therefore remains unclear to date.

The aim of this paper is to describe and taxonomically define all four members of the *C. rugosa* Group, based on well-preserved and hitherto undescribed trace fossil material from four localities in central and southern Bolivia. The excellent preservation of the trace fossils enables a discussion on the validity of Seilacher's (1970) original ichnospecies

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differentiation. In contrast to most of the published *Cruziana*-bearing successions, the herein-presented specimens of *C. furcifera*, *C. goldfussi*, *C. rouaulti* and *C. rugosa* occur in successions where the biostratigraphy is well known based on indicative body fossils and/or the lithostratigraphic position allows the definition of the age of the investigated specimens. Based on these data it is possible to test the biostratigraphic validity of the *Cruziana rugosa* Group for Bolivia and discuss its use for Peri-Gondwanan successions worldwide.

2. Geological setting

Shallow marine siliciclastic deposits are common in the Ordovician successions of Andean Bolivia (Suarez Soruco, 1976). They were deposited on the low-inclined eastern flank of a basin delimiting the Brazilian Shield in the west (Gohrbandt, 1992). Nowadays, these siliciclastic deposits form a major part of the Eastern Cordillera in NW Argentina, Bolivia and southern Peru. The sediments show a cumulative thickness of more than 15 km and can be regarded as the most prominent Ordovician succession worldwide (Egenhoff, 2000).

The age of the shallow-marine siliciclastic deposits in the Eastern Cordillera of southern to central Bolivia decreases from south to north (Suarez Soruco, 1976). In the Tarija region (Fig. 1), the clastic deposits are of early Tremadoc to Arenig age. Around Potosí and Sucre, Middle and some Upper Ordovician sediments are exposed, whereas near Cochabamba, sediments of Caradoc and Ashgill age (Upper Ordovician) predominate (Suarez Soruco, 1976). Unfortunately, neither the litho- nor the biostratigraphy is well established, except for the Tarija area (Rivas, Fernandez & Alvaro, 1969; Erdtmann *et al.* 1995; Maletz & Egenhoff, 2001). All presumably lower Llanvirn (Middle Ordovician) sediments around Potosí and Sucre are grouped into the Capinota Formation, and every lithostratigraphic unit of supposed upper Llanvirn and Caradoc age is referred to as the Anzaldo Formation (Fig. 2) (Rivas, 1971; Suarez Soruco, 2000). The top of the Ordovician succession is marked by the non-fossiliferous sandstone-dominated San Benito Formation of assumed Ashgill age. Its prograding geometries are interpreted to reflect the sea-level fall in the late Ashgill due to the onset of the Hirnantian glaciation (Sempere, 1995).

3. The Bolivian material of the *Cruziana rugosa* Group

In the Bolivian Ordovician, all four species of the '*Cruziana rugosa* Group' (Seilacher, 1970) occur and are described in detail below. Several specimens of *C. rugosa*, *C. furcifera*, *C. rouaulti* and *C. goldfussi* have been collected in the localities of Sella, Cienega, Tipa Jara and Liriuni (Fig. 1). Liriuni, in the vicinity

Figure 1. Location of the study area in central and southern Bolivia. The four investigated localities are marked with black stars.

of Cochabamba, is incorporated in this study because it represents the type locality of *C. rugosa* and *C. furcifera* (d'Orbigny, 1839, 1842).

With exception of the specimens in Figure 5a and b which are property of the Museo 'Alcide d'Orbigny', Cochabamba (Bolivia), all specimens are stored in the collections of the Freie Universität Berlin, Institut für Geologische Wissenschaften, Fachrichtung Geologie, Berlin-Lankwitz (Germany).

3.a. Description of the members of the *C. rugosa* Group

Ichnogenus *Cruziana* d'Orbigny 1842

Cruziana rugosa d'Orbigny 1842

Figure 3a–c

Material. Thirty-five specimens from three localities, some well preserved, mainly as positive hyporeliefs in yellow-reddish or light brown massive and fine-grained (to silty) sandstones from the Chaupi Cancha creek and from a neighbouring locality near the old

Figure 2. Stratigraphic overview scheme for the Ordovician succession in central (left) and southern (right) Bolivia. Note that in the study area of southern Bolivia only Lower Ordovician rocks are exposed, whereas in central Bolivia, Middle and Upper Ordovician strata also crop out. The biostratigraphy of the southern Bolivian units is much better constrained than in central Bolivia due to the higher abundance of indicative fossils in the south. The black stars indicate the approximate stratigraphic position of the four investigated localities. Data compiled from Egenhoff (2000), C. Hildebrandt (unpub. Diploma thesis, Univ. Freiberg, 2003), Rivas, Fernandez & Alvaro (1969) and Suarez Soruco (2000).

cemetery of the village of Sella, north of Tarija, SE Bolivia (Fig. 1). *Cruziana rugosa* is in general the most common ichnospecies in the Rumi Orkho Formation in Sella (Fig. 3a). Further measured, and in part photographed, material remains *in situ* in the field, particularly some big slabs in natural position in the outcrop Chaupi Cancha near Sella. One further well-preserved specimen (Fig. 3b) has been collected from a Middle to Upper Ordovician locality near Tipa Jara (Aiquile, SE Cochabamba province). *Cruziana rugosa* also occurs in the Liriuni section (Caradoc).

Description. Mostly deep and relatively short bilobate trace fossils showing a pronounced median furrow and steep vertical declining margins. Size usually varying

in a relatively small range of about 50 to 90 mm in width (each lobe ~20–30 mm wide). D'Orbigny (1842) measured a width of 85 mm for the type species. Only in a few cases, the traces may be smaller (~12–20 mm in width). Length relatively short (~100–200 mm long; after d'Orbigny, 1842, 150 mm), straight and vertically curved digging traces resulting in the typical domed casts preserved in positive hyporelief.

The surface of both lobes shows the impressions of the endopod grouped in sets of 5 to 12 individual impressions running parallel or in varying V-angles (up to about 90°), that is, transverse to the trace axis/median furrow. The orientation of the scratch marks (endopod impressions) indicates a procline ploughing of the trace originator through the sediment. *C. rugosa* is characterized by coarse transverse ridges (or bundles) about 5 to 15 mm wide superimposing the digit impressions (single scratches) and are arranged in opposite pairs at an angle of about 90° to the median furrow.

Cruziana furcifera d'Orbigny 1842

Figures 3d, e, 4a, b

Material. Thirteen specimens from all four localities, preserved in positive hyporelief in a massive yellowish-brown silty sandstone from the Sella locality (Fig. 3d). In addition to the collected material (Figs 3e, 4a, b), other non-collectable specimens from the Middle to Upper Ordovician localities of Cienega and Tipa Jara have been examined in the field.

Description. Relatively large (~20–100 mm wide and up to some decimetres long) bilobate trace fossils in the form of usually straight and relatively flat-domed moulds (casts in positive hyporelief preservations). Median furrow pronounced, lobe margins, in contrast to *C. rugosa*, gently and smoothly downsloping to the median furrow as well as to the lateral trace margins. The lobes show rhythmically and periodically occurring flat swellings running transversally to the median line, causing an undulation of the primary straight scratches. The orientation of the scratches indicates an opisthocline ploughing of the trace originator through the sediment. They are in V-shaped orientation, mostly with acute angle in relation to the trace axis, in some cases showing also nearly longitudinal (parallel) position to the trace axis and usually superimposing each other, which results in the characteristic reticulate patterns on the surface of the lobes.

Remarks. *Cruziana furcifera* was interpreted to represent merely a variant of *C. rugosa* and *C. goldfussi*, respectively, reflecting different behaviour modes or preservational aspects (Kolb & Wolf, 1979). However, the lack of the transverse bundles and the flat-dipping lateral trace margins without any signs of genal spine grooves, especially in well-preserved specimens

Figure 3. (a) *Cruziana rugosa* d'Orbigny 1842. Well preserved specimen showing the typical bundle-shaped ornamentation of the endopodal lobes in *Cruziana rugosa*. Specimen SE-98-31; Arenig, Rumi Orkho Formation, Sella near Tarija (southern Bolivia); (b) *Cruziana rugosa* d'Orbigny 1842, from the Tipa Jara locality demonstrating the typical steeply domed lobes with the prominent scratch mark pattern, superimposed by bundle-shaped wrinkles on the lobe surface. Specimen Ai-01-52, Middle (?) to Upper Ordovician, Anzaldo Formation; (c) *Cruziana rugosa* d'Orbigny 1842. Poorly preserved but significant specimen with typical bundle-shaped wrinkles superimposing scratch mark patterns on the lobe surfaces. Specimen Lir-01-II, upper Anzaldo Formation (Caradoc), Liriuni locality (Central Bolivia); (d) *Cruziana furcifera* d'Orbigny 1842. Two examples of this ichnogenus showing the flat to slightly domed endopodal lobes with a (*C. goldfussi*-like) scratch mark ornamentation but without lateral genal spine grooves. The specimen SE-98-24 (big photo) is partly crossed by a hyporelief of *Palaeophycus* isp. The magnification in the inset photo (specimen SE-98-37) demonstrates the typical reticulate shape of the scratch mark pattern on the lobes. Arenig, Rumi Orkho Formation, Sella; (e) *Cruziana furcifera* d'Orbigny 1842. Well preserved specimen showing the flat to slightly domed endopodal lobes with the reticulate scratch mark pattern. The *Cruziana* trace is cut by a vertical (non-arthropod) trace of the *Skolithos* type (arrow). Specimen CC-01-04, Anzaldo Formation, Cienega. Scale bar equals 2 cm in each of the photos.

which are frequently accompanied by well-preserved specimens of *C. rugosa* and *C. goldfussi* in the same layer, demonstrate the ichnotaxonomically distinctive characteristics of *C. furcifera*.

Cruziana goldfussi Rouault 1850 (Lebesconte, 1883)

Figures 4c–e, 5a, b

Material. One specimen (SE-98-30; Fig. 4c) well preserved as positive hypo-relief in yellowish-brown

silty sandstone from the Arenig of the Rumi Orkho Formation of Chaupi Cancha near Sella (leg.: P. Diaz, Tarija). A further two specimens from the Middle to Upper Ordovician succession of Cienega and Tipa Jara, central Bolivia, could not be collected (Fig. 4d, e) because they formed part of a large boulder. Two other specimens from the Liriuni locality (Caradoc) are stored in the collection of the Museo 'Alcide d'Orbigny' in Cochabamba (Fig. 5a, b).

Figure 4. (a) *Cruziana* cf. *furcifera*. A poorly preserved *Cruziana furcifera*. The lateral structure on the left-hand lobe edge could also represent a remnant of a genal spine groove and therefore this specimen might be interpreted as a 'transition' to *C. goldfussi* only due to preservational aspects. Specimen Ai-01-50, Middle (?) to Upper Ordovician, upper Anzaldo Formation, Tipa Jara; (b) *Cruziana furcifera* d'Orbigny 1842 and *Cruziana goldfussi* Rouault 1850 (Lebesconte, 1883). Specimen from Tipa Jara with *Cruziana furcifera* (left) and *Cruziana goldfussi* showing the characteristic genal spine groove preserved as lateral ridge (arrow). Specimen Ai-01-51, Middle (?) to Upper Ordovician, upper Anzaldo Formation, Tipa Jara; (c) *Cruziana goldfussi* Rouault 1850 (Lebesconte, 1883). Specimen showing the flat endopodal lobes and the typical lateral genal spine grooves (arrow) in *Cruziana goldfussi*. Specimen SE-98-30; Arenig, Rumi Orkho Formation, Sella; (d) *Cruziana goldfussi* Rouault 1850 (Lebesconte, 1883). Specimen showing the typical flat lobes with the remains of a genal spine groove preserved along the upper lobe (arrow). Specimen CC-01-15, Anzaldo Formation, Cienega; (e) *Cruziana goldfussi* Rouault 1850 (Lebesconte, 1883). Well preserved specimen of *C. goldfussi* showing the flat lobes laterally accompanied by the typical ridges (genal spine grooves) in positive hyporelief preservation. Specimen Ai-01-53, Middle (?) to Upper Ordovician, Anzaldo Formation, Tipa Jara. Scale bar equals 2 cm in each of the photos.

Description. Large and straight-running bilobate trace fossils about 60 to 70 mm in total width. Both endopodal lobes slightly domed, rather flat but separated by a pronounced median furrow. The orientation of the scratch marks (endopod impressions) indicates an opisthocline ploughing of the trace originator through the sediment as well as slight undulation and reticulate patterns caused by criss-crossing and superimposing

of the endopodal markings. Generally, this trace type is very similar to *C. furcifera* but always with distinct lateral furrows (ridges in positive hyporeliefs, each ~5–6 mm wide) running along the trace margins. These lateral grooves or ridges have been interpreted as possible genal (and/or pygidial) spine grooves or traces of the carapace margin dragging on the substrate (Birkenmajer & Bruton, 1971).

Figure 5. (a) *Cruziana goldfussi* Rouault 1850 (Lebesconte, 1883). Excellently preserved specimen of *C. goldfussi* showing the typical large and very flat lobes with the lateral ridges (genal spine grooves). Specimen: Museo 'Alcide d'Orbigny', Cochabamba (Bolivia); upper Anzaldo Formation (Caradoc), Liriuni locality; (b) *Cruziana goldfussi* Rouault 1850 (Lebesconte, 1883). Well-preserved specimen from the same locality as (a), demonstrating the characteristics of *C. goldfussi*. Museo 'Alcide d'Orbigny', Cochabamba (Bolivia), upper Anzaldo Formation (Caradoc), Liriuni locality; (c) *Cruziana rouaulti* Lebesconte 1883. Unicate slab from the Sella locality with numerous non-arthropod traces and arthropod scratch marks (e.g. *Monomorphichnus* isp.) and a well-preserved positive hyporelief of *Cruziana rouaulti*. The specimen demonstrates the typical flat and usually unornamented endopodal lobes with lateral genal spine grooves (arrow) of *Cruziana rouaulti*. The inset photo shows the middle part of the same specimen under another illumination angle to demonstrate the faintly preserved scratch marks close to the median furrow (arrow). Specimen SE-98-32; Arenig, Rumi Orkho Formation, Sella. Scale bar equals 2 cm in each of the photos.

Remarks. As the majority of ichnotaxobases of *C. goldfussi* are quite similar to those of *C. furcifera*, except in terms of the pleural furrows (genal spine grooves), *C. goldfussi* should be strictly used only for those specimens that clearly show these characteristic lateral furrows (ridges) coinciding with a *C. furcifera*-like lobe ornamentation (see also emended diagnosis by Baldwin, 1977). Similar genal spine grooves are known only from the much smaller and almost unornamented *C. rouaulti* (see description below), and from *C. semiplicata* Salter 1853, which, however, shows another characteristic pattern of endopodite and lateral exopodite scratches on the lobes (see Seilacher, 1960; Seilacher & Crimes, 1969; Mángano, Buatois & Aceñolaza, 1996). Moreover, *C. semiplicata* seems to be exclusively restricted to the Upper Cambrian.

Cruziana rouaulti Lebesconte 1883

Figure 5c

Material. One excellently preserved specimen in a greyish-brown massive and fine-grained to silty sandstone from the area around Sella (Locality: Cerro de la Santa Cruz Loma, Sella Formation; specimen SE-98-32; Fig. 5c).

Description. Bilobate trace fossil that consist of two narrow endopodal lobes. Traces straight or gently curved and up to some decimetres in length, with pronounced median furrow, in well-preserved specimens also showing narrow lateral furrows (ridges, each ≤ 1 mm wide) along the trace margins (trace of genal spines?). Endopodal lobes are generally smooth, without prominent endopodal scratches. Only excep-

tionally well-preserved specimens show faint and thin transversally running ridges that have mostly a right-angled ($\sim 90^\circ$) orientation to the trace axis. Endopodal lobes are each about 5–7 mm wide (total trace width ~ 10 –15 mm). The lobes are flat (about 2–4 mm high), resulting in a characteristic flat rectangular-appearing cross-section of the traces.

Remarks. The ichnotaxonomy of *C. rouaulti* is not well founded and is an ongoing matter of discussion. Their similarity to other ichnogenera (e.g. *Didymaulichnus*, *Rouaultia*) has been repeatedly discussed and has resulted in contradictory synonymies (e.g. Péneau, 1946; Crimes, 1970; Young, 1972; Durand, 1985).

3.b. Is a clear taxonomic differentiation of four ichnospecies of the *Cruziana rugosa* Group possible?

The taxonomic criteria for the separation of the different ichnospecies of *Cruziana* remain critical. Seilacher (1992) distinguished 34 ichnospecies of *Cruziana* from the Lower Cambrian to the Lower Carboniferous of Gondwana, mainly by their different scratch patterns. Within the *C. rugosa* Group, *C. furcifera* is said to be the least distinctive, with the widest palaeogeographic distribution (Seilacher, 1970). However, according to Seilacher (1992), the differentiation of the four *C. rugosa* Group ichnotaxa is often problematic and even Seilacher (1992) states that distinguishing them can sometimes be regarded a 'matter of opinion'.

Our material from Bolivia, however, allows a clear distinction between individual *C. rugosa* Group

ichnospecies. Two main characteristic and distinctive elements, the lateral (genal spine) furrow or ridge in *C. goldfussi* and the steep vertically declining margin exclusive of *C. rugosa* were excluded in Kolb & Wolf's (1979) study. In no case in our collected material from Bolivia, nor in the numerous specimens observed in the field, was the typical steep *C. rugosa* margin found together with a lateral spine groove. The few cases of *C. rugosa* with supposedly lateral grooves cited by Kolb & Wolf (1979) from the literature (Crimes & Marcos, 1976; Bergström, 1976) seem to be misinterpretations; following the diagnosis of Seilacher (1970), the specimen figured in Crimes & Marcos (1976, pl. 2, fig. a) is not a *C. rugosa* as it lacks the typical bundle-like ornamentation and shows a genal spine groove which is clearly not significant for *C. rugosa*. The specimen in Bergström (1976, fig. 6A) is a poorly preserved and therefore rather problematic specimen of the (?) *C. rugosa* type showing remains of a lateral spine groove, but not the typical bundle-shaped ornamentation of *C. rugosa* on the lobe surfaces, and it therefore represents rather a *Cruziana* aff. *goldfussi*. Bergström (1976, fig. 6D) illustrates a putative *C. rugosa*, but due to clearly visible lateral spine grooves, it is obviously a poorly preserved *C. goldfussi*. *C. rouaulti*, which also possesses lateral ridges, differs clearly from *C. goldfussi* by its much smaller and very flat lobes lacking the characteristic reticulate scratch patterns. The exclusively Cambrian ichnotaxon *C. semiplicata*, which is also characterized by genal spine grooves, displays a more complex lobe ornamentation consisting of very characteristic endo- and exopodal scratches (Seilacher, 1990). Therefore only a taxonomic uncertainty exists in terms of the somewhat transitional characteristics of *C. furcifera* and poorly preserved *C. goldfussi* specimens lacking preservation of their lateral spine grooves. Also, Mángano, Buatois & Moya (2001) describe *C. furcifera* that rarely grades laterally into *C. goldfussi*. Their figure 3a, however, only documents an intergradation of these two well-distinguishable ichnotaxa similar to our Bolivian material. It therefore remains unclear whether the transition of one *Cruziana* ichnotaxon into the other as mentioned by Mángano, Buatois & Moya (2001) is partly due to preservational aspects of the Argentinian material, or if it really represents an intergradation of two ichnospecies. But even though a transition should exist between *C. furcifera* and *C. goldfussi*, intermediate specimens are the exception rather than the norm and should not lead to the abandonment of the ichnospecies concept for the *Cruziana rugosa* Group (Pickerill, Romano & Meléndez, 1984). It is concluded that the ichnotaxonomic characteristics allow a clear distinction between the four members of the *C. rugosa* Group in well-preserved material, and therefore, based on the excellently preserved Bolivian *Cruziana* specimens, Seilacher's (1970) ichnospecies are here considered valid.

Table 1. Stratigraphic occurrence of *Cruziana* and associated trace fossils in Bolivia

Locality	Stratigraphy	Trace fossils
Liriu	Upper Anzaldo Formation Upper Ordovician (Caradoc)	<i>Cruziana rugosa</i> <i>Cruziana furcifera</i> <i>Cruziana goldfussi</i> <i>Palaeophycus</i> isp.
Tipa Jara	Anzaldo Formation Middle(?) to Upper Ordovician (Caradoc)	<i>Cruziana rugosa</i> <i>Cruziana</i> cf. <i>furcifera</i> <i>Cruziana goldfussi</i>
Cienega	Upper Capinota and Anzaldo formations Middle to Upper Ordovician (Darriwilian to Caradoc)	<i>Cruziana furcifera</i> <i>Cruziana goldfussi</i> <i>Palaeophycus</i> isp. <i>Skolithos</i> isp.
Sella	Rumi Orkho Formation Lower Ordovician (Arenig)	<i>Cruziana rugosa</i> <i>Cruziana furcifera</i> <i>Cruziana goldfussi</i> <i>Palaeophycus</i> isp. (?) <i>Rusophycus</i> isp. <i>Monomorphichnus</i> isp.

4. The bio- and lithostratigraphic position of the Bolivian *Cruziana* ichnoassemblages

The four localities where the Bolivian members of the *C. rugosa* Group have been collected correspond to differing litho- and/or biostratigraphic levels within the Ordovician succession. Each of the localities is discussed in detail below. Furthermore, a list of the trace fossil assemblage is provided for each of the investigated sections (Table 1).

4.a. Sella (21°22'30" S, 64°41'49" W)

The Lower Ordovician Rumi Orkho Formation (Fig. 2; Egenhoff, 2000; F. Schönián, unpub. Diploma thesis, Humboldt Univ., 2000), exposed near the village of Sella, about 30 km north of Tarija, yielded the majority of the trace fossils described in this paper. Along with several non-arthropod traces, mainly *Palaeophycus* isp. (see specimen in Fig. 3d), and non-specific arthropod scratch marks, the Rumi Orkho ichnofossil assemblage contains common *C. rugosa*, less abundant *C. furcifera*, and rare *C. goldfussi* and *C. rouaulti* (Figs 3a, d, 4c, 5c).

In the Rumi Orkho Formation, the *Cruziana* ichnofossils occur in interbedded sand-, silt- and mudstones. The succession is dominated by sandstones; the pelitic intercalations are relatively thin and contain a large amount of silt.

A number of relatively well-preserved graptolites were found in the Rumi Orkho Formation at Sella (Fig. 6). The graptolites are flattened and generally do not show internal structural details. However, a determination is still possible from this only slightly tectonized material. Maletz, Kley & Reinhardt (1995) illustrated specimens of *Baltograptus* sp. cf. *B. deflexus*, while Egenhoff (2000) referred material to *Baltograptus* sp. cf. *B. deflexus* and *Baltograptus minutus*. The presence of these graptolites helps to delimit the age of the Rumi Orkho Formation. Maletz & Egenhoff (2003)

Figure 6. Graptolites from the Rumi Orkho Formation at Sella. (a) SE 01, *Baltograptus minutus* (Tullberg). (b) SE 02, *B. minutus* (Tullberg). (c) SE 03, *Baltograptus* sp. cf. *B. deflexus* (Elles & Wood). Specimens at Geological Institute, Freie Universität Berlin, Germany. Magnification $\times 10$, indicated by two dots at a distance of 1 mm near proximal end of all specimens.

and Egenhoff, Maletz & Erdtmann (2004) established a *Baltograptus minutus* Biozone in the mid-Arenig of southern Bolivia, correlatable with the Australasian Chewtonian. *B. minutus* is common in the Arenig of the Tøyen Shale Formation of Scandinavia (J. Maletz, unpub. Ph.D. thesis, Technische Univ. Berlin, 1992), where the faunal association indicates a restriction to the mid-Arenig (Chewtonian of the Australasian faunal succession), while *Baltograptus* sp. cf. *B. deflexus* appears in the upper part of the *Pendeograptus fruticosus* interval in Scandinavia, comparable to the Bendigonian 3–4 (see VandenBerg & Cooper, 1992) and ranges into the *B. minutus* Biozone. The Rumi Orkho Formation thus corresponds to the *Baltograptus minutus* Biozone and is of mid-Arenig age.

4.b. Cienega (19°03'30" S, 64°59'45" W)

The locality is situated at the northern end of the village of Cienega, north of the main road between Sucre and Tarabuco. *Cruziana* ispp. occurs at several levels within an 1150 m thick interval of the Capinota and Anzaldo formations. Both units consist of intercalated sand-, silt- and mudstones separated by a fault originated during the Andean Orogeny (Cenozoic). The Anzaldo Formation displays a high sandstone–pelite ratio of about 2:1, whereas the underlying Capinota Formation is dominated by mudstones (sandstone–pelite ratio of about 1:3).

The majority of the specimens of *Cruziana* ispp. from this locality are rather poorly preserved, but some specimens show sufficient significant details for their taxonomic identification. As at Sella, the ichnofossils

Figure 7. Pygidium of *Neseuretus* aff. *sanlucasensis* Přibyl & Vaněk, 1980 from the lower portion of the succession exposed at Cienega. Scale bar equals 2 cm. Specimen CC-01-02, stored at Geologisches Institut, Freie Universität Berlin, Germany.

occur as casts at the base of some centimetre-to decimetre-thick fine-grained sandstone beds.

The arthropod ichnofossil assemblage in both stratigraphic units is characterized by abundant *C. furcifera* and *C. goldfussi* (Figs 3e, 4d) accompanied by poorly preserved non-arthropod traces sometimes cutting through the *Cruziana* type traces (*Palaeophycus* isp. and *Skolithos* isp., see specimen in Fig. 3e). No true *Cruziana rugosa* was found at the Cienega locality.

4.b.1. Biostratigraphic age of the Capinota Formation at Cienega

The Capinota Formation at Cienega yielded a single relatively well-preserved steinkern of a pygidium of *Neseuretus* (*Neseuretus* aff. *sanlucasensis* Přibyl & Vaněk, 1980) (Fig. 7). The genus *Neseuretus* ranges from the Arenig to the basal Ashgill (see Turvey, 2002). *Neseuretus sanlucasensis* is exclusively known from the Llanvirn of San Lucas (*Hoekaspis* zone) of Bolivia (Přibyl & Vaněk, 1980). However, it is still a matter of debate if *Neseuretus sanlucasensis* can be included in the genus *Neseuretus*, or if it should be assigned to the genus *Aristocalymene* (Turvey, 2005). The reason is that the material figured in Přibyl & Vaněk (1980) is incomplete and its cephalic morphology is therefore not completely understood (Turvey, 2005). But as the cladistic analysis undertaken in Turvey (2002) shows *Neseuretus sanlucasensis* to belong to the stem group of the later *Neseuretinus*–*Vietnamia* clade, it is more probable that the Bolivian specimen from the lower part of the Cienega succession indicates a late Arenig to Llanvirn age.

4.b.2. Conodonts from the uppermost Anzaldo Formation at Cienega

At the top of the Anzaldo Formation at the locality of Cienega, carbonate concretions contain conodont

Figure 8. Conodont elements from the uppermost Anzaldo Formation from the Cienaga locality. Scale bars equal 100 μm . (a) *Semiacontiodus* sp., SMF 69990, lateral view, (b) *Drepanoistodus?* sp., SMF 69991, lateral view, (c–f) fragments of multidenticulate processes of *Erismodus* sp., (c) isolated denticle, SMF 69992, (d) isolated denticle, SMF 69993, (e) inner view of process fragment, SMF 69994, (f) inner view of process fragment, SMF 69995, (g) *Erismodus* cf. *E. quadridactylus* (Stauffer), Sb element postero-lateral view, SMF 69996.

faunas. The small assemblage includes fragmentary elements of *Erismodus* cf. *E. quadridactylus* (Stauffer) (Fig. 8g), isolated cusps and denticles of *Erismodus* elements (Fig. 8c–f), one fragment of *Drepanoistodus?* sp. (Fig. 8b) and some coniform elements of *Semiacontiodus* sp. (Fig. 8a). Unfortunately, no index taxa characteristic for a certain conodont zone were recovered. One special problem of *Erismodus* material is that the processes break easily at the boundaries between the different denticles (see, for example, the narrow connections between the denticles in the fragment in Fig. 8f). As a consequence, large cusp fragments occur together with isolated denticles in a way similar to material of *Coryssognathus* (Miller & Aldridge, 1993) or in material of the giant conodont *Promissum pulchrum* described by Aldridge *et al.* (1995) from the Soom shale of South Africa. Bedding plane assemblages of *Promissum* in different stages of preservation well display that denticles sitting on basal tissue can easily be isolated (collections of R. A. Aldridge, University of Leicester). In a similar way, *Coryssognathus* elements fall apart and discrete cones in the collections often represent denticles broken from the multidenticulated processes but also discrete cones previously attached only to some basal tissue.

In hyaline material recovered from the Anzaldo Formation, fragments of cusps or large denticles without any preserved base can neither be attributed to *Erismodus* nor to *Semiacontiodus*. Only a few elements with complete, separate bases are placed into *Semiacontiodus* sp. (Fig. 8a) and large denticles sitting on some part of a process fragment (Fig. 8c–f) can (based on their association with *Erismodus* elements)

tentatively be interpreted as fragments of *Erismodus* (Fig. 8c–f) but usually could not be distinguished from similar fragments of *Polycaulodus* or *Chirognathus duodactylus* Branson & Mehl 1933. In general, the apparatus structure of *Erismodus* is still under study and there are many problems in understanding the different species of this ‘plastic’ taxon. A modern diagnosis of *Erismodus* was given by Sweet (1982), who provides a detailed synonymy of *Erismodus quadridactylus* (Stauffer). In the Bromide Formation of Oklahoma, *Erismodus arbuckelensis* Bauer, *Erismodus quadridactylus* and *Erismodus typus* Branson & Mehl 1933 occur and are distinguished by the character of their Sa elements (J. A. Bauer, unpub. Ph.D. thesis, Ohio State Univ. 1987; Bauer, 1994). In contrast to the smoothly rounded posterior side of the cusp in *E. typus*, *E. quadridactylus* is laterally and posteriorly costate like *E. arbuckelensis* but far less compressed (Bauer, 1994, p. 363). This is also a typical feature of the other elements in the *E. quadridactylus* apparatus (Sweet, 1982, pp. 1040–2, pl. 1, figs 25–30) and well recognizable in the figured Sb(?) element from the Anzaldo Formation. Because no diagnostic Sa element was recovered, the fragmentary material from the Anzaldo Formation is illustrated as *Erismodus* sp. (fragments illustrated on Fig. 8b–f) or *E. cf. E. quadridactylus* (in the case of a Sb element displaying a posterior–anteriorly compressed cusp with one posterior and sharp antero-lateral costaet costa, Fig. 8g). One badly preserved element which may represent a drepanodiform element of a *Drepanoistodus?* sp. (Fig. 8b).

The type of the limited hyaline fauna in the upper Anzaldo Formation is quite comparable to faunal assemblages described from the Santa Gertrudis Formation in northern Argentina. There, Sarmiento & Rao (1987, pp. 90–2, pl. 1, figs 1–10, pl. 2, figs 1–10) described *Erismodus quadridactylus* for the first time from the clastic Gondwana succession of the Eastern Cordillera. From the coeval Capillas Formation in the Sierra de Zapla, an association of *Erismodus*, *Erraticodon* and *Plectodina* together with the agnathan fish *Saccambaspis janvieri* is mentioned by Albanesi & Astini (2002) and Albanesi & Moya (2002). More diverse faunas illustrated by Albanesi in Moya *et al.* (2003, p. 21, figs 12.1–12.17) from the Santa Gertrudis Formation in the Gallinato Creek section of the Mojoro Range in the Eastern Cordillera include *Bryanthodina typicalis* Stauffer 1935, *Plectodina* n. sp., *Erismodus* cf. *E. gratus* (Moskalenko), *Erismodus typus* Branson & Mehl 1933, *Erismodus quadridactylus*, *Icriodella* n. sp. A, *Polyscaulodus* sp. and *Semiacontiodus* sp. This assemblage also included no useful zonal index taxa and was placed by Albanesi & Ortega (2002, p. 149, fig. 1) into a ‘non-nominated interval’ ranging from the basal *Eoplacognathus lindstoemi* subzone of the *Pygodus serra* zone through the top of the *Baltoniodus gerdæ* subzone of the *Amorphognathus tvaerensis* zone (Baltic zonation) or from the lower *Chabagnathus sweeti* through the top of the *E. quadridactylus* zone (North American Midcontinent zonation).

However, *Erismodus quadridactylus* (Stauffer, 1935) represents an important taxon ranging from the Mohawkian *E. quadridactylus* zone through the *Plectodina tenuis* zone in Sweet’s North American chronostratigraphic scheme (Sweet, 1984, 1988) and therefore ranges up into slightly younger levels than proposed for the non-nominated interval (Fig. 9) by Albanesi & Ortega (2002). The range of the taxon in North America correlates to upper fauna 7 through lower fauna 9 in the older literature (Sweet, Ethington & Barnes, 1971), which is equivalent to the uppermost *Baltoniodus gerdæ* subzone of the *Amorphognathus tvaerensis* zone through the uppermost *Baltoniodus alobatus* subzone of the *A. tvaerensis* zone (Sweet, 1984, 1988) and in terms of North American stages it includes approximately the upper part of the Turinian and the lower part of the Chatfieldian (Fig. 9). There is no detailed description of the conodont succession in the Mojotoro Range published yet, but the faunas of the Santa Gertrudis Formation and the Anzaldo Formation may be at least partly coeval. If the *Erismodus* faunas occur in approximately the same time interval in western Peri-Gondwana, a Turinian age (possibly *E. quadridactylus* zone) seems to be plausible.

4.c. Tipa Jara near Aiquile (18°12′00″ S, 65°17′30″ W)

The *Cruziana* ichnofossils in the surroundings of the village of Tipa Jara (SE of Cochabamba, central

Figure 9. Stratigraphic chart showing the range of *Erismodus quadridactylus* (vertical black bar) according to Sweet (1984, 1988) and the ‘non-nominated interval’ (white box) of Albanesi & Ortega (2002) for the faunas of the Santa Gertrudis Formation in the Mojotoro Range of northern Argentina.

Bolivia) occur in the lower to central part of an approximately 2400 m thick, largely tectonically undisturbed section (Fig. 10), exposing the Middle to Upper Ordovician Anzaldo Formation (M. Maldonado & M. Montaña, unpub. Geobol report, 1967). The Tipa Jara succession consists of intercalated mud-, silt- and sandstones with sand- and siltstone-rich facies where the *Cruziana* specimens occur (C. Hildebrandt, unpub. Diploma thesis, Univ. Freiberg, 2003). The *Cruziana* traces are abundant in several decimetre-thick beds in three stratigraphic levels within overall *Skolithos*-dominated facies often associated with *Palaeophycus* isp. The fossil material from this locality consists of two rather poorly preserved specimens of *Cruziana* cf. *furcifera* (Fig. 4a, b), one specimen of *C. goldfussi* (Fig. 4e) and one excellently preserved specimen of *C. rugosa* (Fig. 3b).

No time-indicative fossils have been found in the entire succession at Tipa Jara so far. However, the conformably overlying San Benito Formation bears Upper Ordovician chitinozoans and lower Ashgill brachiopods (M. A. Perez Leyton, unpub. report, 1986; Suarez Soruco & Benedetto, 1996). The ichnofossils occur about 850 m below the base of the San Benito Formation (Fig. 10), which is in the upper third of the Anzaldo Formation at this locality. The Llanvirn–Caradoc boundary is believed to be

Figure 10. Overview section of the Ordovician succession in central Bolivia based on C. Hildebrandt (unpub. Diploma thesis, Univ. Freiberg, 2003), Rivas (1971) and Suarez Soruco (1976, 2000), and a detailed section from the Tiza Jara locality (C. Hildebrandt, unpub. Diploma thesis, Univ. Freiberg, 2003). The black arrows indicate stratigraphic portions where *Cruziana* occurs within the Anzaldo Formation. The last *Cruziana* was found in Tiza Jara about 850 m below the base of the Ashgill San Benito Formation.

located in the central part of the Anzaldo Formation (M. Maldonado & M. Montaña, unpub. Geobol report, 1967). This argues for a Caradoc age of the *Cruziana* traces from Tiza Jara.

4.d. Liriuni near Cochabamba (17°17'06" S, 66°17'40" W)

The ichnofauna studied in 2001 in several outcrops near the village of Liriuni about 20 km north of Cochabamba (central Bolivia) is clearly dominated by *C. goldfussi* (Fig. 5a, b). These are frequently associated with abundant individuals of *Palaeophycus* isp. that often cut through the *Cruziana*. Branisa (1965,

p. 78, pl. 7) figured a large slab from Liriuni with *Cruziana furcifera*, obviously accompanied by several individuals of *C. goldfussi*. D'Orbigny (1842) figured an excellently preserved specimen of *C. rugosa* from the Cochabamba region. Seilacher (1992) also has reported *C. rugosa* from the Cochabamba region. A rather poorly preserved but still significant specimen showing the typical bundle pattern on the surface from our locality at Liriuni is shown in Figure 3c. The trace fossils occur at numerous levels within an at least 500 m thick interval within the upper Anzaldo Formation that is dominated by decimetre-thick sandstones. Branisa (1965) referred to the Liriuni succession as belonging to the uppermost Caradoc. Recent acritarch and brachiopod data in the surroundings of Cochabamba (Gagnier *et al.* 1996) support a Llanvirn to Caradoc age for the Anzaldo Formation. As the Liriuni locality represents the uppermost part of the Anzaldo Formation only shortly below the contact with the lower Ashgill San Benito Formation (Suarez Soruco & Benedetto, 1996), it is likely that the *Cruziana* faunas indeed have a late Caradoc age.

4.e. Implications for *C. rugosa* biostratigraphy

This study proves that in Bolivia, *C. furcifera*, *C. goldfussi* and *C. rugosa* occur in Arenig to Caradoc strata and therefore have a limited biostratigraphic relevance, indicating solely an Ordovician age when found in this part of Gondwana. These findings are in good agreement with earlier descriptions by Steinmann & Hoek (1912), who figured a specimen of *C. furcifera* from Palca del Tunari near Cochabamba which probably has a middle to late Caradoc age (Gagnier, 1993; Gagnier *et al.* 1996). Only the taxon *C. rouaulti* seems to be restricted to Lower Ordovician successions in Bolivia. Its rareness even within these strata, however, inhibits a well-based statement on its true biostratigraphic range.

On a worldwide basis, the *C. rugosa* Group is not restricted exclusively to Lower Ordovician sediments, in contrast to Seilacher's (1992) statement, although it remains unclear what Seilacher (1970, 1992) defines as Lower Ordovician as he subdivides the Ordovician period only into Lower and Upper. *C. rugosa*, *C. furcifera* and *C. goldfussi* do occur in Middle Ordovician successions in the Armorican Massif (Delgado, 1886; Lessertisseur, 1955; Seilacher, 1992) and in North Africa (Desio, 1940; Seilacher, 1992). *C. rugosa*, however, seems to be in fact restricted to a middle Tremadoc to Arenig interval throughout Gondwana. Although one study exists reporting *C. rugosa* from 'Lower Silurian strata' of the Yangtze platform (Yunnan) in southern China (Yin, 1932), recent graptolite findings by B.-D. Erdtmann (pers. comm. 2003) support an Early Ordovician rather than a Silurian age of these sediments.

5. Discussion

The present study is not the first to question the reliability of the '*Cruziana rugosa* Group' as a biostratigraphic indicator for the Lower Ordovician. Based on rather poor material judging from their figured specimens, Magwood & Pemberton (1990) reported the occurrence of *C. rugosa* together with *C. furcifera* and *C. goldfussi* from the Lower Cambrian (Atdabanian) Gog Group of Alberta, Canada, and have generally questioned the value of Seilacher's biostratigraphic approach. The specimens figured in Magwood & Pemberton (1990, p. 731, fig. 3A, B, C), however, are not really convincing: the '*C. goldfussi*' in their figure 3B shows no sign of any lateral ridges and looks very similar to the '*Cruziana rugosa*' shown in figure 3C which again shows no transversal bundles and only very flat and diffuse declining margins (that is, not *C. rugosa*).

Seilacher (1994) presented better preserved fossil material from British Columbia, Canada, and has rejected the criticism made by Magwood & Pemberton (1990). Based on the well-preserved specimens, Seilacher (1994) showed that the Gog Group specimens belong to a Cambrian *Cruziana* type (*C. pectinata*) having a distinct scratch pattern, and they therefore do not contradict his *Cruziana* stratigraphy. It should be taken into consideration that *C. rugosa* has not yet been reported from strata older than middle Tremadoc and therefore seems to have a biostratigraphic value in defining sediments younger than early Tremadoc in age.

The Ordovician successions in Bolivia where *Cruziana* ichnofossils occur are generally dominated by sandstones and are referred to as the 'Grès Armoricaïn Facies' by Seilacher (1992). This type of facies is widely distributed throughout Peri-Gondwana in the Lower Ordovician, but Upper Ordovician strata worldwide often exhibit finer-grained sediments. The Bolivian sections then correspond to a nearshore environment rarely preserved from the Late Ordovician time interval. Therefore, the exclusive occurrence of the *C. rugosa* Group in Lower Ordovician strata may be just an artefact of facies distribution in stratigraphy. Consequently, the occurrence of *C. rugosa* Group traces with the exception (?) of *C. rouaulti* probably does not represent a powerful biostratigraphic tool for subdividing otherwise non-fossiliferous Ordovician sandstones.

At least in South America (W. Gondwana), *C. rugosa*, *C. furcifera* and *C. goldfussi* therefore do not seem to be suitable as index fossils for a subdivision of the Ordovician system (*sensu* Seilacher, 1970, 1992, 1994; Baldwin, 1977; Crimes, 1968). Only the possibly very restricted biostratigraphic distribution of the rare taxon *C. rouaulti* (Fig. 5c) remains a matter of speculation. In fact, this ichnospecies is hitherto only known from the Lower Ordovician (Arenig) of North

Africa and Armorica and from the lower Arenig of Bolivia as demonstrated in the present study.

The palaeobiogeographic distribution of *Cruziana*-type arthropod traces may reflect the changing distribution patterns of a certain group of arthropod trace originators. Probably several large benthic trilobite taxa, highly adapted and specialized to shallow-marine siliciclastic environments, occurred successively in the Lower Palaeozoic on the passive continental margins of Gondwana.

6. Conclusions

(1) The taxonomic re-evaluation presented herein supports the subdivision of the *C. rugosa* Group into *C. furcifera*, *C. goldfussi*, *C. rouaulti* and *C. rugosa* as originally defined by Seilacher (1970). Based on our well-preserved specimens from Bolivia, we show that each of the four ichnospecies indeed displays sufficient characteristics, such as the presence or absence of lateral spine grooves, scratch patterns etc. to distinguish them unequivocally, even in the field. The statistical approach of Kolb & Wolf (1979), negating a subdivision of the *C. rugosa* Group based on measurable criteria, therefore has to be considered invalid. This is because the V-angle of scratches as well as the amount of scratches per centimetre used in that study are not valuable parameters in differentiating ichnospecies of the *Cruziana rugosa* Group and should possibly not be considered a prime criterion for distinguishing *Cruziana* ichnogenera in general.

(2) In Bolivia, *C. furcifera*, *C. goldfussi* and *C. rugosa* occur in Lower to Upper Ordovician strata. Therefore, they cannot be regarded as a reliable biostratigraphic indicator for the Lower Ordovician at least for Bolivia and adjacent regions. Although up to now only known from Bolivia, it should be expected that in the sand-rich 'Grès Armoricaïn' facies these three ichnospecies may occur worldwide. The obvious diachronous appearance of *C. furcifera*, *C. goldfussi* and *C. rugosa* within and outside Gondwana casts doubts on the real value of a *Cruziana*-related biostratigraphy for a global subdivision and correlation within the Ordovician System. However, the *Cruziana rugosa* Group can be used to identify Ordovician strata in Bolivia.

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