

The first record of Hirnantian Ostracoda in South America: implications for the biostratigraphy and paleozoogeography of the Paraná basin

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Abstract.—Herein is reported the first occurrence of ostracodes from the Iapó Formation, an uppermost Ordovician unit of the Rio Ivaí Group in the Paraná basin, Brazil. Two ostracode species were identified in the Três Barras Farm section: *Harpabollia harparum* (Troedsson, 1918) and *Satiellina paranaensis* Adôrno and Salas in Adôrno et al., 2016 were recovered from dropstone-bearing shale overlying glaciogenic diamictites, a feature typical of Hirnantian (uppermost Ordovician) strata throughout Gondwana. The taxonomy of the Genus *Harpabollia*, as well as its type species *Harpabollia harparum*, was reviewed, and emended and new diagnoses were respectively proposed for each taxon. Occurrences of *Harpabollia harparum* and *Satiellina* species were common in areas influenced by cold waters. Additionally, the occurrence of *Harpabollia harparum*, an index species to the uppermost Ordovician of several stratigraphic units in Baltica and southern Gondwana, allowed us to infer a Hirnantian age for the deposits of the Iapó Formation. Other than being associated with *Harpabollia harparum* in Iapó Formation of the Paraná basin, *Satiellina paranaensis* is also found in lower levels of the Vila Maria Formation; therefore, these are also considered Hirnantian in age. Above these lower levels of the Vila Maria Formation, a well-dated Rhuddanian (lowermost Llandovery, Silurian) palynomorph assemblage is observed within the formation. These occurrences are evidence of a continuous process of sedimentary deposition during the Ordovician–Silurian transition in the Paraná basin.

Introduction

In this work, we report the first occurrence of the ostracode *Harpabollia harparum* (Troedsson, 1918), a key constituent of Hirnantian (uppermost Ordovician) assemblages and an index fossil for that stage (Meidla et al., 2013), in a lithologic unit of Brazil—the Iapó Formation of the Rio Ivaí Group, Paraná basin. Paleozoogeographical and paleoecological implications of this new record are also briefly discussed herein. In addition, we report a new record of the ostracode *Satiellina paranaensis* Adôrno and Salas in Adôrno et al., 2016, which has implications for the stratigraphic framework of the Ordovician–Silurian transition in the Paraná basin.

Marine Ordovician fossil representatives of the Ostracoda Latreille, 1802 are present in the stratigraphic record of a wide range of latitudes (Williams et al., 2003; Mohibullah et al., 2012; Meidla et al., 2013) and environments (Vannier et al., 1989; Williams and Siveter, 1996). Since the Early Ordovician (Salas et al., 2007, 2018; Williams et al., 2008), ostracodes have presented a global geographical distribution, colonizing marine

environments from shore faces to continental slopes (Braddy et al., 2004). Although the record of Ordovician ostracodes is large, with hundreds of species described, it is very irregular among land masses and age intervals of that period. Whereas hundreds of species have been described from the paleocontinents of Baltica (Meidla, 1996; Tolmacheva et al., 2001; Tinn et al., 2006), Laurentia (Williams and Siveter, 1996), Avalonia (Landing et al., 2013), Siberia (Melnikova, 1986, 2011), and Ibero-Armorica (Vannier, 1986; Vannier et al., 1989), the record is much more restricted in Gondwanan basins (Schallreuter, 1988; Hinz-Schallreuter and Schallreuter, 2007; Salas et al., 2007; Salas, 2011; Salas and Vaccari, 2012).

In the case of Hirnantian ostracode species, records are even fewer and restricted mainly to countries of the modern Baltica region (Lithuania, Latvia, and Estonia) and Sweden (collectively known as Baltoscandia), with some isolated occurrences in Austria, Canada, Czech Republic, and Poland (Mohibullah et al., 2012; Meidla et al., 2013; Truuver and Meidla, 2015). During that age, prevailing latitude-related climatic gradients created a marked biogeographical segregation among low-, mid-, and high-latitude assemblages of brachiopod, graptolite, and chitinozoan faunas (Benedetto et al., 2013). However, only two distinct types of Hirnantian ostracode assemblages

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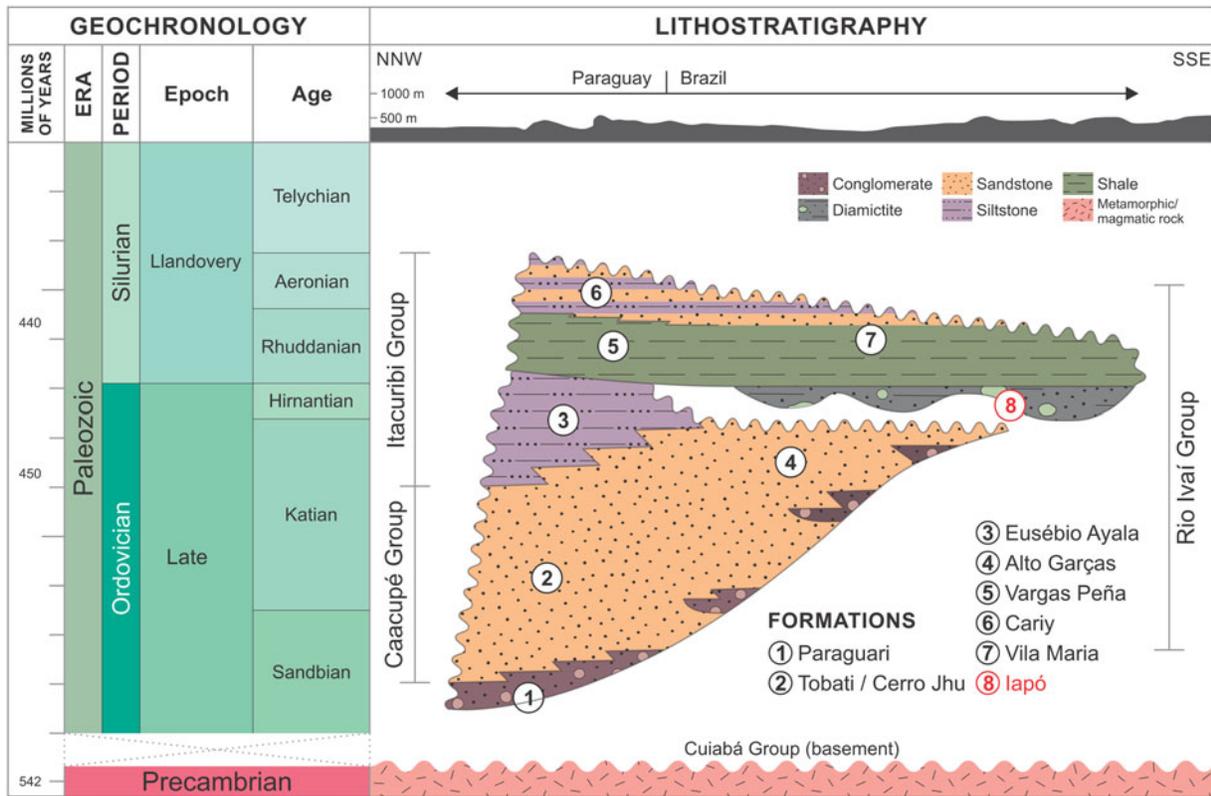


Figure 1. Chronolithostratigraphic chart of the Rio Ivaí Group, Paraná basin, Brazil, according to Assine et al. (1998) and Adorno et al. (2016).

are observable worldwide: low-latitude warm-water assemblages, typified by *Medianella aequa* (Stumbur, 1956), and mid- to high-latitude cool-water assemblages, characterized by *Harpabollia harparum*. One important exception to this scenario is the Baltic region, which was in a low- to mid-latitude upheaval zone during the Hirnantian. The consequent influence of the cold-water “Livonian tongue” in the region favored the establishment of a cold-water assemblage in latitudes lower than expected for such faunas (Meidla, 2007; Meidla et al., 2013).

In South America, despite considerable investigation and sampling of Hirnantian successions, no ostracode faunas have been recorded so far, possibly because glacial events dominated the geological history of Gondwanan lithologies during that stage, as exemplified by records from the Andina Central and Precordillera basins in Argentina and the Maranhão and Paraná (i.e., the Iapó Formation) basins in Brazil (Alvarenga et al., 1998; Benedetto et al., 2015). Occurrences of *Satiellina parnensis* and *Conchoprimitia brasiliensis* Adorno and Salas in Adorno et al., 2016 in shale levels at the base of the Vila Maria Formation, which overlies the Iapó, imply an Ordovician age for both the Iapó and lowermost Vila Maria formations because *Satiellina* Vannier, 1986 and *Conchoprimitia* Öpik, 1935 are restricted to the Ordovician Period. Coupled with the absence of an unconformity between the Iapó and Vila Maria formations, as well as the presence of glacial diamictite strata, this feature suggests a Hirnantian age for the interval (Adorno et al., 2016). However, no index fossil typical of the Hirnantian has been observed in the Iapó–Vila Maria transition until now.

Geological setting

The Paraná is an intracratonic basin that encompasses territories of south-central Brazil, eastern Paraguay, northeastern Argentina, and central-west Uruguay. The Rio Ivaí Group is the lowermost Phanerozoic stratigraphic unit in the basin and Brazil, spanning from the Upper Ordovician to the Llandovery (Assine et al., 1994; Milani et al., 2007). The Rio Ivaí Group comprises, from bottom to top, the Alto Garças, Iapó, and Vila Maria formations and is exposed mainly at the northern border of the basin in Central-West Brazil (Alvarenga et al., 1998).

The Iapó Formation is composed of diamictites and fine-grained facies with dropstones, deposited during a glacial advance/retreat cycle (Assine et al., 1994, 1998; Alvarenga et al., 1998). The Hirnantian age of the formation (Assine et al., 1994, 1998) is based, among other features, on stratigraphic correlation with other glacial diamictite-bearing units, such as the Nhamundá and Ipú formations in Brazil (Caputo, 1998; Vaz et al., 2007), the Zapla in Argentina, the Cancañiri in Bolivia, and the Eusebio Ayala in Paraguay (Benedetto et al., 2013, 2015; Cishowolski et al., 2019). The fine-grained facies of the Iapó Formation have so far provided fossiliferous occurrences of archeogastropods and brachiopods such as *Kosoidea australis* Zabini et al., 2019, an inarticulate brachiopod species of the Hirnantian–Llandovery genus *Kosoidea* Havlíček and Mergl, 1988 (Zabini et al., 2019, 2021) (Fig. 1).

Samples studied in the present work were recovered from the Três Barras Farm section of Adorno et al. (2016), one of the best-known outcrops of the Iapó Formation and the only

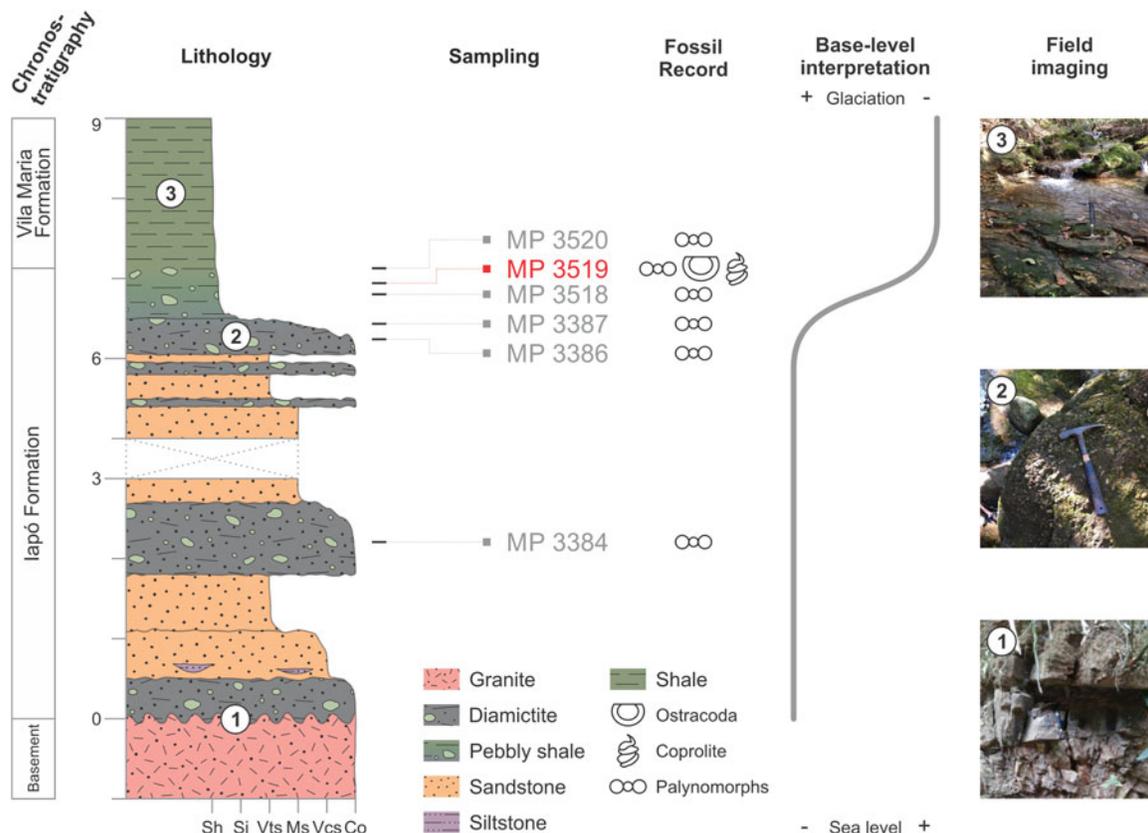


Figure 2. Lithologic log of the Três Barras Farm section, Bom Jardim de Goiás, State of Goiás, Brazil. (1) Contact between the Iapó Formation and the basement. (2) Diamictite facies of Iapó Formation. (3) Shale facies of the Vila Maria Formation. Symbols used herein follow the Federal Geographic Data Committee (2006).

one dated through radiometric analysis (Mizusaki et al., 2002). This section is approximately 14 m in stratigraphic thickness, the lower 9.5 m of which are sedimentary deposits of the Iapó Formation, represented by massive polymictic glacial diamictites and shale with dropstones in a greenish-colored shale–sandstone matrix (Fig. 2). Just above these lies a thin layer of sandstone. The sedimentary deposits of the Iapó Formation at Três Barras Farm unconformably overlie granitic rocks that form the basement of the Paraná basin; above them lie the black shale levels of the Vila Maria Formation in gradational contact.

Materials and methods

Field campaigns for this work were conducted between 2016 and 2018, during which were performed the lithostratigraphic log (descriptive criteria follow Miall, 1985) and systematic sampling of the Três Barras Farm section. The main sampling area was at a subsection of Três Barras along the Jacaré Creek, located ~20 km south of the Town of Bom Jardim de Goiás, State of Goiás, Central-West Brazil (16°26.615'S, 52°5.825'W) (Fig. 3). One sample yielding ostracodes was collected at 6.95 m in the section MP-3519, from a level composed of shale with dropstones and sandstones.

The methodology for extraction of ostracodes from rock samples followed Adôrno et al. (2016): First, they were separated from the main bulk of samples by hand cutting ~0.3 cm³

blocks containing specimens. After that, each specimen was excavated from its blocks and cleaned with 1 mm syringe needles under a Leica ES4 stereoscopic microscope. Selected specimens were coated with gold on a Leica EM SCD500 high vacuum film deposition system and photographed and analyzed using a JEOL NeoScope JCM-5000 scanning electron microscope at the Micropaleontology Lab (LabMicro) of the University of Brasília (UnB), Brazil.

Images of specimens were measured, whenever possible, by using CorelDRAW X6 and the Windows 7 Calculator software. Due to a preservation artifact that led to dislocation between valves and abrasion, both the length and height of CP-852 and CP-902 were approximated up to points respectively assumed as the hypothetical posterior end and ventral margins of the right valve.

Repository and institutional abbreviation.—All illustrated specimens are housed at LabMicro at the Research Collection of the Museum of Geosciences (MGeo), under the codification “CP” (from the Portuguese *Coleção de Pesquisa*) and numbers 851; 852; 853; 902; 903; 904; 905.

Systematic paleontology

The taxonomy of *Harpabollia harparum* (Troedsson, 1918) and *Satiellina paranaensis* Adôrno and Salas in Adôrno et al., 2016 as well as their stratigraphic and paleogeographical

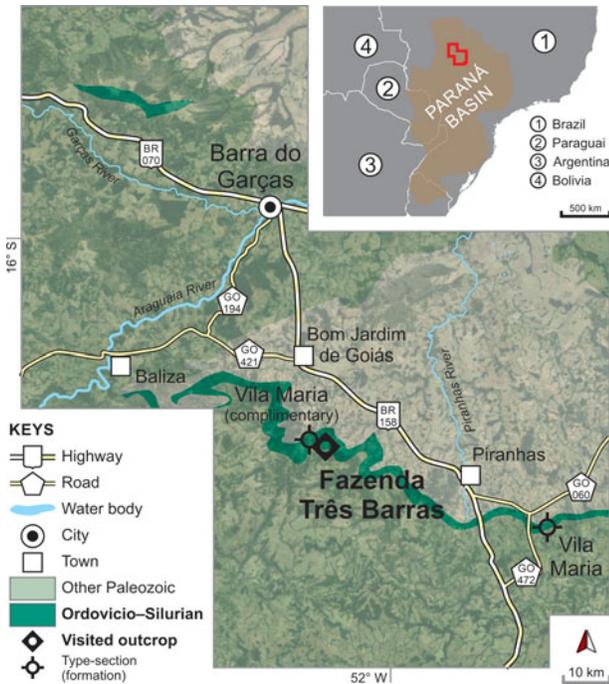


Figure 3. Geographical map showing the location of the Três Barras Farm section and Paleozoic surfaces around the Bom Jardim de Goiás Municipality, State of Goiás, Brazil. Other Paleozoic units in the area include the Furnas and Ponta Grossa (Devonian) and the Aquidauana formations (Carboniferous), while the Ordovician–Silurian is represented by the Vila Maria and Iapó formations (Alvarenga et al., 1998). Symbolization standards follow the Federal Geographic Data Committee (2006).

distribution are presented here. Supraordinal and ordinal taxonomies follow Liebau (2005) while the subordinal taxonomy is based on Mohibullah et al. (2013). The terminology for morphological features of ostracode carapaces and valves is from Scott (1961) and Vannier et al. (1989).

- Subclass Ostracoda Latreille, 1802
- Superorder Podocopomorpha Kozur, 1972
- Order Palaeocopida Henningsmoen, 1953
- Suborder Binodicopina Schallreuter, 1972
- Superfamily Drepanelloidea Ulrich and Bassler, 1923
- Family Bolliidae Bouček, 1936
- Genus *Harpabollia* Schallreuter, 1990

Type species.—*Bollia harparum* Troedsson, 1918 (Schallreuter, 1990), by original designation.

Diagnosis (emended).—Genus of Bolliidae characterized by the following features: elongate, L₂ and L₃ connected ventrally by a prominent U-shaped lobe; L₁ and L₄ as subvertical ridges, remarkably weaker than L₂ and L₃ and connected ventrally by a pseudovelum, forming a U-shaped groove parallel to the ventral margin; a wide, nonlobate area in the posterior region of the lateral valve surface.

Remarks.—The generic diagnosis largely follows Schallreuter (1990) but with modifications to avoid the original use of the morphological term “zygal crista.” Historically, names used for said structure have widely diverged (Kesling, 1951;

Henningsmoen, 1953, 1965; Martinsson, 1962; Weber and Becker, 2006), even after Schallreuter (1973) made a clear distinction between lobes and sulci (formed by folding of the valve and demonstrating the opposite structures on the internal surface) and ornamental features such as cristae (formed by thickening of the shell and not visible internally). In *Harpabollia* Schallreuter, 1990, the ventral connection of the two lobes demonstrates a clearly lobal character, being prominent also in internal molds (see Schallreuter 1990, fig. 2-2). This justifies the amendment of the generic diagnosis.

Melnikova (2010) suggested *Harpabollia* might be a junior synonym of *Pseudozygobolbina* Neckaja in Abushik et al. (1960). However, *Harpabollia* differs from *Pseudozygobolbina* by several features, including, in lateral view, greatest height of the carapace at a median (versus anterocentral) position, a less tumid (versus more tumid) L₄ lobe that is positioned far (versus reaches closer) from the posterior end of the valves, L₂ and L₃ lobes not projecting (versus projecting) beyond the hinge line, and smooth (versus punctate) ornamentation around and over part of L₂ and L₃.

Harpabollia harparum (Troedsson, 1918)
Figure 4.1–4.5

- 1918 *Bollia harparum* Troedsson, p. 12, pl. 2, figs. 19, 20.
- ?1934 *Bollia harparum*; Bassler and Kellett, p. 72.
- 1966 *Bollia* sp.; Havlíček and Vaněk, p. 61.
- ?1968 *Bollia mezvagarensis*; Gailite, p. 132.
- ?1970 *Bollia mezvagarensis*; Gailite, p. 23.
- ?1979 *Bollia harparum*; Nilsson, p. 11.
- ?1982 *Bollia mezvagarensis*; Ul’st et al., p. 121.
- 1985 *Bollia mezvagarensis*; Sztejn: p. 72, pl. 4, fig. 8.
- ?1985 *Quadrijugator harparum*; Schönlaub, p. 66.
- 1986 *Quadrijugator?* *harparum*; Vannier, p.107, figs. 30D, E, 31a, b.
- ?1988 *Quadrijugator harparum*; Schönlaub, p. 109.
- 1988 *Harpabollia harparum*; Schallreuter and Krůta, p. 100.
- 1990 *Harpabollia harparum*; Schallreuter, p. 122, fig. 2:1–3.
- 1992 *Bollia mezvagarensis*; Sidaravičienė, p. 166, pl. 53, fig. 10.
- 1995 *Harpabollia argentina*; Schallreuter, p. 2, pl. 83, fig. 1.
- 1996 *Harpabollia harparum*; Meidla, p. 80, pl. 15, fig. 3.
- [non] 1999 *Harpabollia harparum*; Gubanov and Bogolepova, p. 419, fig. 2J.
- 2007 *Harpabollia harparum*; Meidla, p. 124, fig. 2a, b.
- 2015 *Harpabollia harparum*; Truuver and Meidla, p. 739, figs. 5.25, 7M, N.
- 2021 *Harpabollia harparum*; Zabini et al., p. 9, fig. 8a.

Lectotype.—Mold of a left valve, no. LO 2904T, from Tommarp, Sweden, currently housed at the Department of Geology of Lund University, Lund, Sweden (Troedsson, 1918).

Diagnosis (new).—Species of *Harpabollia* characterized by the following features: valves that are more convex anteriorly; L₂

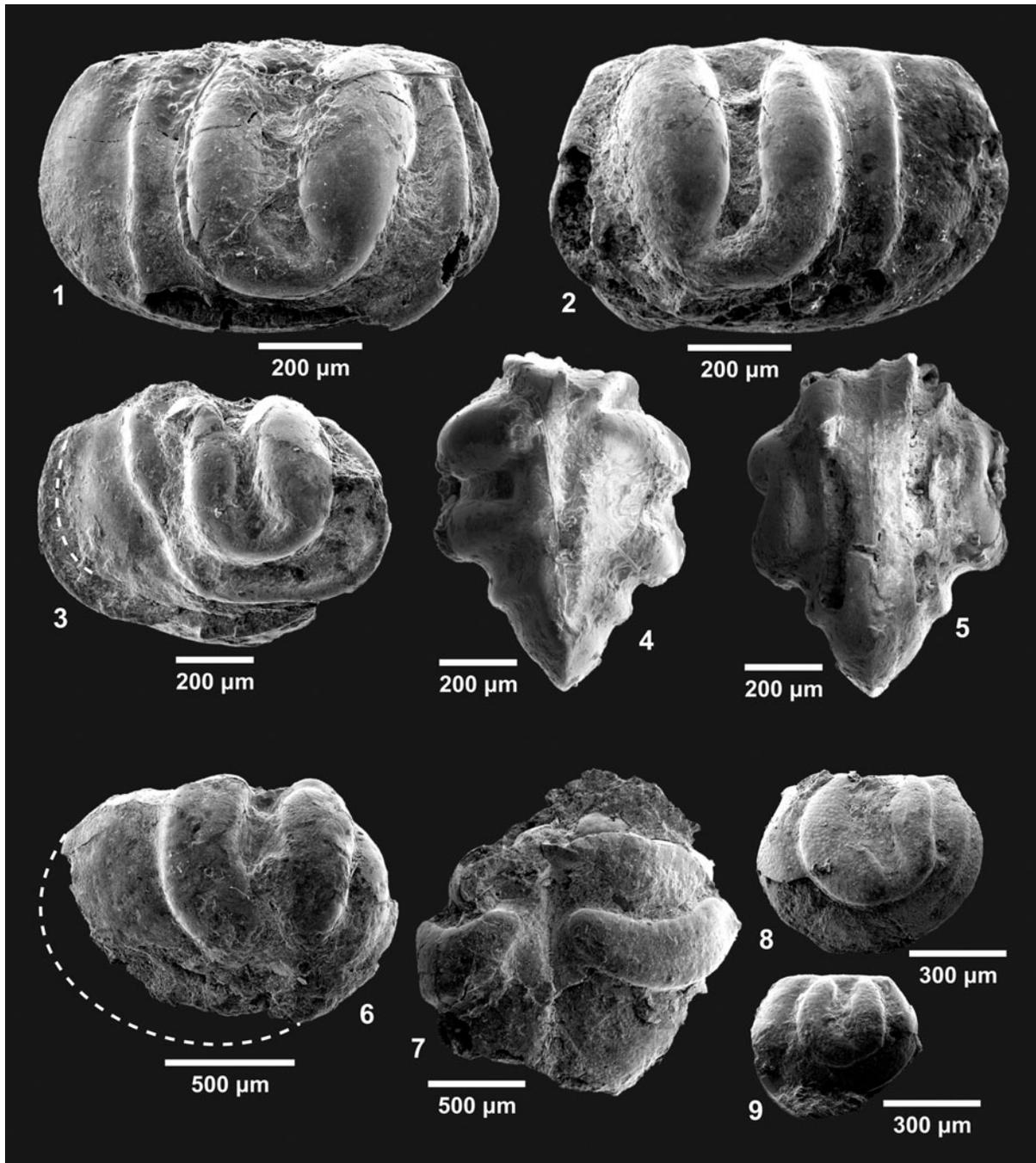


Figure 4. Ostracode species found in the Iapó Formation, Rio Iváí Group, Paraná basin, Brazil. (1–5) *Harparollia harparum* (Troedsson, 1918). (1, 2, 4, 5) Adult carapace (CP 851): (1) right lateral view; (2) left lateral view; (4) dorsal view; (5) ventral view. (3) Adult carapace (CP 852) displaying a preserved connection between L_1 and L_4 lobes (the dotted line marks the approximate posterior end of the right valve). (6–9) *Satiellina paranaensis* Adorno and Salas in Adorno et al., 2016: (6), adult carapace (CP-902), right lateral view (the dotted line marks the approximate posterior end and dorsal margins of the carapace); (7) (CP-903) dorsal view of disarticulated valves; (8) juvenile valve (CP 904), right lateral view; (9) juvenile valve (CP 905), right lateral view.

and L_3 with elongated bulb-like dorsal swellings; L_2 is more prominent than L_3 and may reach slightly beyond the dorsal margin; L_1 and L_4 as subvertical ridges; L_1 nearly parallel to the anterior margin.

Occurrence.—Late Ordovician: Katian, Precordillera Argentina basin (Salas, 2007), Rio Sassito Formation sensu Keller and Lehnert (1998), Argentina, San Juan Province, Sassito Creek

(Schallreuter, 1995); Hirnantian: (1) Scandinavian basin sensu Harris et al. (2004), Sweden: (1a) upper part of Lindegård mudstone (Calner et al., 2013), Skåne County, Röstånga (“localities 5a and 3i”) and Tommarp (“locality 17”) (Troedsson, 1918), and (1b) possibly Loka Formation, Östergötland County, Borensult locality (Meidla, 2007), (2) Livonian basin sensu Harris et al. (2004), Kuldiga Formation: (2a) Latvia, Ventspils Municipality, Mežvagari and Piltene,

Kuldīga Municipality, Adze and Remte, Saldus Municipality, Blidene and Sturi, Engure Municipality, Dreimani (Gailite, 1970), Pavilosta Municipality, Riekstini (Brenchley et al., 2003), and Jūrmala Municipality, Jūrmala (Meidla et al., 2011), and (2b) Estonia, Valga County, Taagepera (Meidla, 1996), and Pärnu County, Ruhnu (Brenchley et al., 2003), (3) Prabuty Formation (Truuver and Meidla, 2015), Poland, Warmińsko-Mazurskie Voivodeship, Dłużec Mały (Sztejn, 1985; Podhalańska, 2014), (4) Carnic basin, Plöcken Formation sensu Corradini et al. (2015), Austria, Carinthia State, “Cellon section” (Carnic Alps) (Schallreuter, 1990), and (5) Prague basin, Kosov Formation sensu Röhlich (2007), Czech Republic, Bohemia (Havlíček and Vaněk, 1966; Schallreuter and Krůta, 1988). The present work expands the lithostratigraphic and geographical distributions of the species to, respectively, the Iapó Formation, Rio Ivaí Group, Paraná basin, and the Três Barras Farm section, Bom Jardim de Goiás, State of Goiás, Brazil.

Materials.—CP-851, adult carapace (length = 0.892 mm; height = 0.574 mm; width = 0.663 mm), CP-852, adult carapace (length \approx 0.862 mm; height \approx 0.542 mm; width nonmeasurable), and CP-853, adult disarticulated valves (nonmeasurable).

Remarks.—The specific identification follows Troedsson (1918). In the present work, we include a specific diagnosis for *Harpabollia harparum* because it is absent from Schallreuter (1990), who solely provided a diagnosis for the genus *Harpabollia*. Some individuals from Baltoscandian strata in Estonia (Meidla, 1996), Poland (Sztejn, 1985; Truuver and Meidla, 2015), and Sweden (Meidla, 2007) differ from the Brazilian ones by their narrower and less tumid L₃ lobe, but the Brazilian morphotype is also present in the Baltoscandian area, as exemplified by other materials from Sweden (Troedsson, 1918) and Austria (Schallreuter, 1990). In a similar way, the weak L₄ lobe also varies rather widely within the pool of figured specimens. This might be due to different levels of preservation, as some of the materials are internal molds and not carapaces or valves. *Bollia mezvagarensis* Gailite, 1970 is strikingly similar to other species of *Harpabollia*, despite its type materials being much larger than *Harpabollia harparum* and *Harpabollia argentina* Schallreuter, 1995. Specimens of *Bollia mezvagarensis* in Sztejn (1985) are of the same size as the ones in Troedsson (1918) and, despite the poor positioning of specimens for illustration in the plates, clearly belong to *Harpabollia harparum*. *Bollia mezvagarensis* in Sidaravičiene (1992) presents a higher length/height ratio than the *Harpabollia harparum* type specimen illustrations in Troedsson (1918) due to electronic deformation of illustrative SEM photographs; otherwise, they clearly belong to *Harpabollia harparum*. Despite being different in size and overall shape, *Harpabollia argentina* is strikingly similar in ornamentation to *Harpabollia harparum*; we consider it to be a juvenile instar form of the species as it is common among binodicipine ostracodes for the juveniles and adults of the same species to share common ornamentation features. Several doubtful attributions in the synonymic list of *Harpabollia harparum* (Bassler and Kellett, 1934; Gailite, 1968; Nilsson, 1979; Ul'st

et al., 1982; Schönlaub, 1985, 1988) are due to such publications not presenting images of specimens evaluated. The only exceptions to this list are Havlíček and Vaněk (1966) and Schallreuter and Krůta (1988), since both materials were evaluated by the author who proposed both the genus *Harpabollia* and the inclusion of *Harpabollia harparum* as its type species (Schallreuter, 1990). The specimen figured in Gubanov and Bogolepova (1999) clearly does not present the lobe pattern of the genus *Harpabollia* and therefore is not synonymous with *Harpabollia harparum*.

Family incertae sedis
Genus *Satiellina* Vannier, 1986

Type species.—*Bollia delgadoi* Vannier, 1983 (Vannier, 1986), by original designation.

Satiellina paranaensis Adôrno and Salas in Adôrno et al., 2016
Figure 4.6–4.9

2014 *Satiellina jamariensis*; Adôrno, p. 28, figs. 4.13.1–17.

2016 *Satiellina paranaensis* Adôrno and Salas in Adôrno et al., p. 383, figs. 4A–F.

Holotype.—Mold of a left valve, CP-634, from Bom Jardim de Goiás Municipality, Brazil, housed in the scientific collections of the Museum of Geosciences at LabMicro, University of Brasília, Brazil (Adôrno et al., 2016).

Occurrence.—Uppermost Ordovician of the Paraná basin, Rio Ivaí Group, Vila Maria Formation, Aldeia Creek section, Bom Jardim de Goiás, State of Goiás, Brazil (Adôrno et al., 2016). The present work expands the lithostratigraphic and geographical distributions of the species to, respectively, the Iapó Formation, Rio Ivaí Group, and the Três Barras Farm section.

Materials.—CP-902, adult carapace (length \approx 1.383 mm; height \approx 1.047 mm; width = 0.603 mm), CP-903, adult disarticulated valves (nonmeasurable), CP-904, juvenile valve (length = 0.704 mm; height = 0.502 mm), and CP-905, juvenile valve (length = 0.532 mm; height = 0.452 mm).

Remarks.—The diagnosis follows Adôrno et al. (2016). In addition, due to the recovery of better-preserved molds that could eventually be separated from the rock matrix, the present work adds imaging of *Satiellina paranaensis* in dorsal view, as well as from juvenile instars of the species. However, new materials display differences from type specimens in Adôrno et al. (2016), namely, a slight furrow in the dorsal half of the L₂ lobe and punctate ornamentation over the lobes; these variations are probably also due to better preservation of the present specimens compared with the type material of *Satiellina paranaensis*.

Discussion

Ostracode assemblages and the age of the Iapó Formation.—The faunas of the Ordovician–Silurian sedimentary deposits of the Paraná basin were known from very isolated and poorly

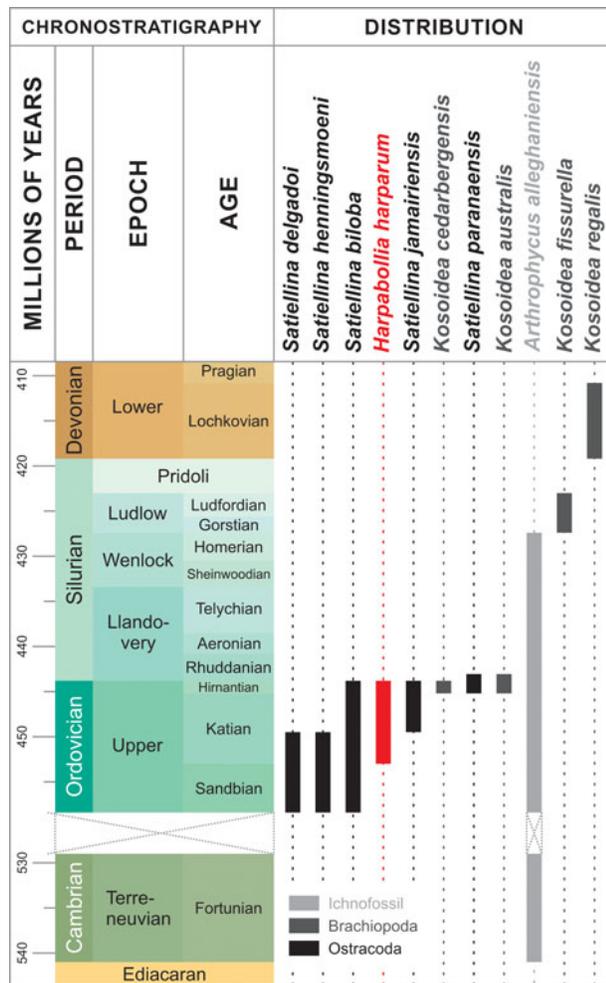


Figure 5. Species diversity and stratigraphic distribution of the ostracod genera *Satiellina* Vannier, 1986 and *Harpabollia* Schallreuter, 1990, the brachiopod genus *Kosoidea* Havlíček and Mergl, 1988, and the ichnospecies *Arthropycus alleghaniensis* (Harlan, 1831).

studied occurrences (Popp et al., 1981) until *Conchoprimitia brasiliensis* and *Satiellina paranaensis* were described by Adôrno et al. (2016) from the Vila Maria Formation. Other than *Satiellina paranaensis*, the genus *Satiellina* comprises four species of Middle–Upper Ordovician distribution throughout Ibero-Armorica, Gondwana, and Baltica: *Satiellina biloba* (Troedsson, 1918), *Satiellina delgadoi* (Vannier, 1983), *Satiellina henningsmoeni* Nion in Robardet et al., 1972, and *Satiellina jamairiensis* Vannier, 1986. Due to its wide geographical distribution and the restricted overall biostratigraphic range of its species, the genus is important for intrabasin strata correlation (Fig. 5).

The present record of the monospecific genus *Harpabollia* and its widespread species, *Harpabollia harparum*, is the first of a taxon whose known distribution is restricted to the Hirnantian (Truuver and Meidla, 2015) in the Rio Ivaí Group of the Paraná basin. *Harpabollia harparum* is the dominant component of the “*Harpabollia harparum* assemblage,” an important and well-known faunal association related to Upper Ordovician cold-water seas around Baltica and the Argentinean region of Gondwana. It is regarded as diagnostic of the Hirnantian by

its co-occurrence with typical members of the *Hirnantia–Dalmanitina* fauna of invertebrates (Meidla, 2007; Truuver and Meidla, 2015). Therefore, this taxon is a powerful tool to constrain the age both of the Iapó Formation and of species associated with it in these deposits, such as *Satiellina paranaensis*. The ostracode fauna herein identified, constituted by *Harpabollia harparum* and *Satiellina paranaensis*, is also the oldest recorded in deposits from Brazil so far and the first of Hirnantian age in South America.

A Hirnantian age for the Iapó Formation can also be inferred by the occurrence (Zabini et al., 2019) of the Hirnantian–Lower Devonian brachiopod genus *Kosoidea*, which comprises the following species: *Kosoidea australis* Zabini et al., 2019, *Kosoidea cedarbergensis* Basset et al., 2009, *Kosoidea fissurella* Havlíček and Mergl, 1988, and *Kosoidea regalis* Havlíček, 1999. In the Três Barras Farm section, *Kosoidea australis* occurs together with *Satiellina paranaensis* and *Harpabollia harparum* in sample MP-3519 of the Iapó Formation. Another important aspect of *Kosoidea australis* is that the species can be found in the Upper Iapó and lower part of the Vila Maria formations (Ordovician) in the Aldeia Creek section of Adôrno et al. (2016) and the COHAB section of Zabini et al. (2019; 2021) (Fig. 6).

Upper portions of the Vila Maria Formation are currently dated as Llandovery, initially on the basis of the presence (Burjack and Popp, 1981) of the Cambrian–early Silurian (Neto de Carvalho et al., 2003) ichnospecies *Arthropycus alleghaniensis* (Harlan, 1831) (also found in the upper part of the Aldeia Creek section [Adôrno et al., 2016]) and later confirmed by palynomorph assemblages (Gray et al., 1985). Additional radiometric Rb–Sr data from the Três Barras Farm section (Mizusaki et al., 2002) indicate an absolute dating of 435.9 ± 7.8 Ma for the shale levels from the Vila Maria Formation, which places it slightly over, but still into the chronologic range of, the late Hirnantian (443.8 ± 1.5 Ma). Therefore, it also agrees (at least partially) with the present brachiopod- and ostracode-based dating for the Iapó and basal Vila Maria formations as Hirnantian.

Paleobiogeography and paleoenvironment analysis.—Paleobiogeographical relationships between Ordovician faunas of the Paraná basin and those from Gondwanan and peri-Gondwanan regions have been previously addressed by Adôrno et al. (2016), who hypothesized the presence of *Satiellina paranaensis* was an indication of the affinities between strata of the Paraná basin and those in northern Africa and Ibero-Armorica. Zabini et al. (2019, 2021) suggested the presence of *Kosoidea* reveals similarities between the Paraná basin and the South African Soom Formation of the Karoo basin (Basset et al., 2009). The occurrence of *Harpabollia harparum* expands the correlation to Baltica, where most of the records of the species are observed (Truuver and Meidla, 2015).

Harpabollia and *Satiellina* were genera typically found in seas that were strongly influenced by nearby ice sheets (although their distribution was not confined to such paleoenvironments [Meidla et al., 2013]); such were the environments found along the continental glacial deposits of the Iapó Formation, as well as in several localities in Gondwana and nearby

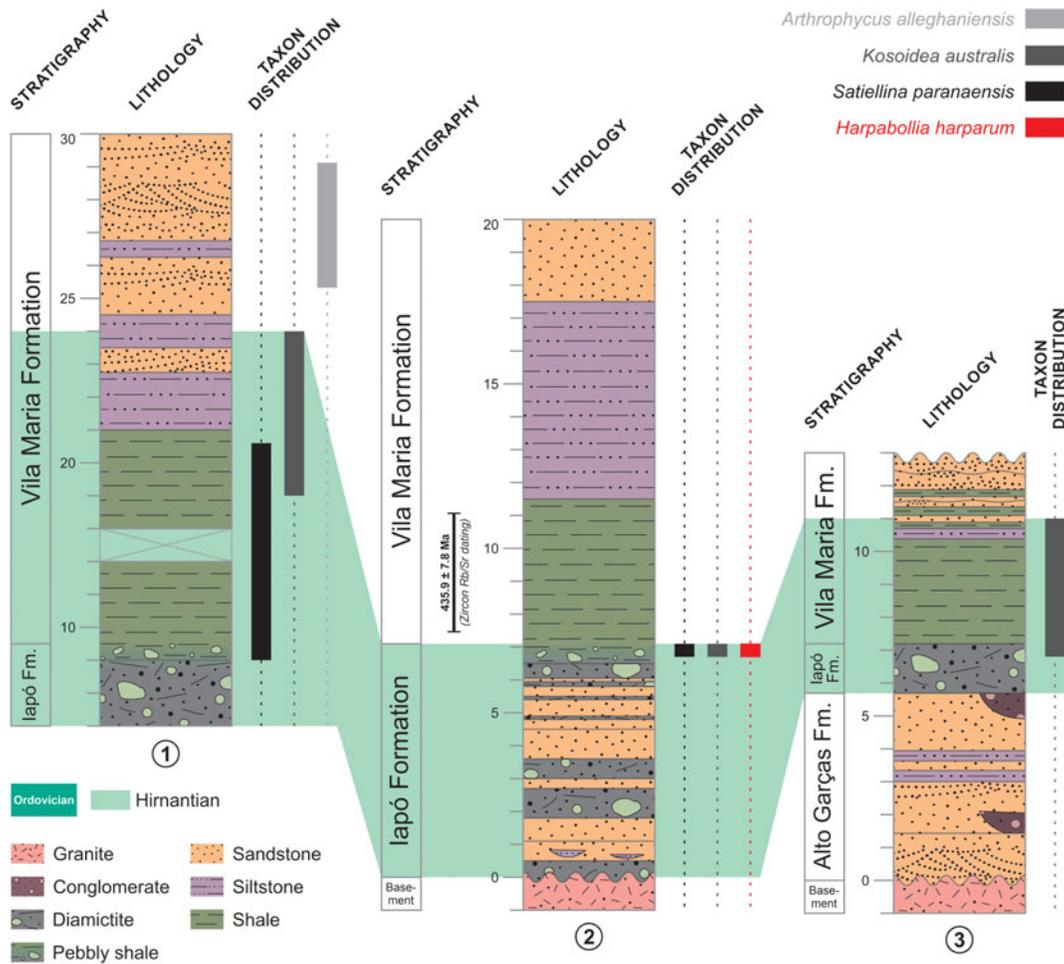


Figure 6. Composite section of the Iapó–Vila Maria interval around the Bom Jardim de Goiás Municipality, State of Goiás, Brazil: (1) Aldeia Creek outcrop; (2) Três Barras Farm outcrop; (3) COHAB outcrop. Co-occurrences of *Harpabollia harparum* (Troedsson, 1918), *Satiellina paranaensis* Adorno and Salas in Adorno et al., 2016, and *Kosoidea australis* Zabini et al., 2019 are exclusive of shale with dropstone levels of the Hirnantian Iapó Formation; the latter two also co-occur at the shale levels of the Hirnantian–Ruddanian basal Vila Maria (Adorno et al., 2016; Zabini et al., 2019), which is also constrained by Rb/Sr dating (Mizusaki et al., 2002). *Arthropycus alleghaniensis* (Harlan, 1831) is found in sandstone/siltstone levels typical of the upper Llandovery (Silurian) Vila Maria (Burjack and Popp, 1981).

continents (Wang et al., 1997; Le Heron and Howard, 2010; Vidal et al., 2011; Benedetto et al., 2013). Deposits of the Iapó are typical of middle- to outer-ramp marine environments (Assine et al., 1998; Benedetto and Muñoz, 2015) and correlate well with glaciogenic deposits in Argentina, Bolivia, Paraguay, Peru, and South Africa.

The faunal affinities between these regions suggest a rapid immigration event for the cold-water species of *Harpabollia* and *Satiellina* along lower- and higher-latitude areas (Vannier, 1986; Meidla, 2007; Scotese, 2014) (Fig. 7). Binodicipine ostracodes such as *Harpabollia* and *Satiellina* rapidly migrated during the Late Ordovician from peri-Gondwana to Avalonia and Baltica propelled by cold-water currents, reaching mostly the deep-shelf (and even shallow-platform) paleoenvironments of these areas. Three possible mechanisms are suggested to explain the migration: (1) active island hopping through Avalonia (Williams et al., 2003) until Baltica, following the pathway opened by the resurgence of the “Livonian tongue” (Meidla et al., 2013); (2) passive long-distance migration through currents (Titterton and Whatley, 1998) along the northernmost Rheic Ocean up to

Ibero-Armorica; (3) passive transport on host animals (Williams et al., 2003) such as cephalopods (very common during the Ordovician) or possibly sharks.

The widespread distribution of *Harpabollia harparum* in the Hirnantian can be traced back to the Katian, when the species was found throughout the Argentinean Precordillera. From there, it seems to have migrated to North and peri-Gondwanan areas during the latest Ordovician. This migration would continue toward the Baltica regions, where Meidla (2007) first described the *Harpabollia harparum* assemblage, typical of Hirnantian cold-water paleoenvironments. Therefore, the occurrence of *Harpabollia harparum* in the Paraná basin represents another step in the pathway proposed for the distribution of the species through Late Ordovician cold-water sea regions. Additional occurrences of *Satiellina paranaensis* and *Kosoidea australis*, associated with *Harpabollia harparum* in the Iapó Formation and in the lower portion of Vila Maria Formation (Adorno et al., 2016; Zabini et al., 2019), indicate a continuous deposition between the Hirnantian–Llandovery intervals or positioned in the lower levels of black shale from Vila Maria Formation.

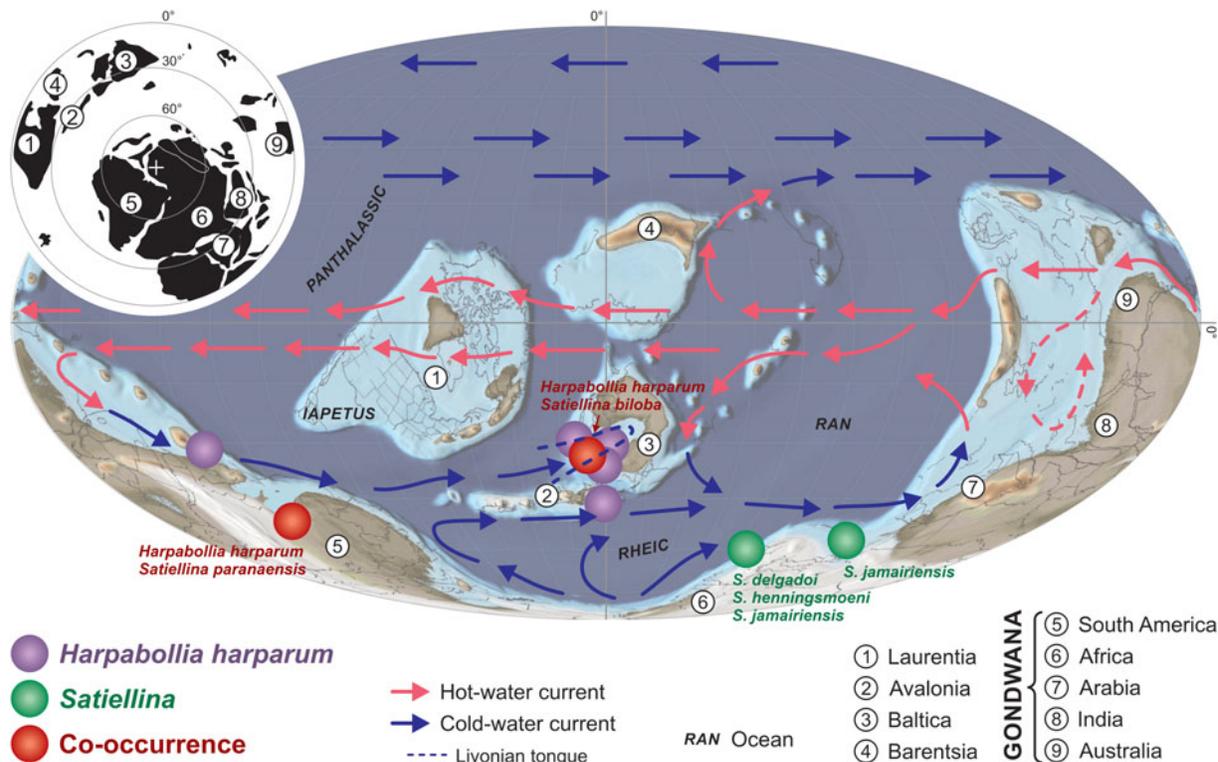


Figure 7. Late Ordovician (Katian–Hirnantian) paleogeographic map (modified from Scotese, 2014 according to Cocks and Torsvik, 2020) showing the latest Ordovician paleozoogeographic distribution of the ostracode genera *Harpabollia* Schallreuter, 1990 and *Satiellina* Vannier, 1986. Notice that species of both genera are confined to regions dominated by cold-water marine currents (Scotese, 2000).

Conclusions

The first occurrence of ostracodes described in the Iapó Formation comprises faunas that were recovered from strata at Goiás State, Brazil. Two species were identified in the present samples: *Satiellina paranaensis*, known from the Vila Maria Formation in the Ordovician–Silurian of the Paraná basin, and, more diagnostic to Hirnantian, *Harpabollia harparum*. The occurrence of this species is a powerful tool to date the Iapó Formation as Hirnantian and to attribute the associated occurrences of *Satiellina paranaensis* to the same chronostratigraphic interval. So far, this is also the oldest ostracode fauna recorded in sedimentary deposits from Brazil and the first Hirnantian ostracod species in South America.

Species of *Harpabollia* and *Satiellina* ostracod genera were cold-water taxa found in marine paleoenvironments strongly influenced by nearby glaciation, such as those along the continental glacial deposits of the Iapó Formation and other parts of Gondwana and Baltica. The faunal affinity between these regions suggests a rapid migration event for both *Harpabollia* and *Satiellina* species, starting from the Argentinean Precordillera during the Katian and reaching other higher-latitude areas (Gondwana), as well as lower-latitude ones (Ibero-Armorica and Baltica, where the *Harpabollia harparum* assemblage was first identified) during the Hirnantian.

Considering occurrence of *Kosoidea australis* in the post-Hirnantian interval in the Vila Maria Formation, it seems that paleoenvironmental changes associated with warming sea temperatures during the Ordovician–Silurian transition have not

extensively affected such faunal distributions in the Rhuddanian interval of Vila Maria Formation.

Acknowledgments

The authors are indebted to the Brazilian Fundação de Apoio à Pesquisa do Distrito Federal (process no. 00193.00002054/2018-91) and the National Council for Scientific and Technological Development (CNPq) (process no. 459776/2014-2) for financial support for the present work, granted between 2018 and 2020. Additional thanks go to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for providing vital access to a vast library of scientific works through its Portal de Periódicos database. We also thank the Center for Research in Earth Sciences, National Scientific and Technical Research Council of the National University of Córdoba, Argentina, for providing laboratory assistance for the study of fossil materials during technical visit by L.R.O. Gonçalves. Finally, we are grateful to the researchers A.M. Leite, A.S. Reis, C. Zabini, and E. Vaccari for the very deep and insightful scientific dialogs that helped enhance this manuscript as well as to the reviewers and the associated editor of the *Journal of Paleontology* for their detailed revision.

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Accepted: 8 August 2021