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The conchostracan subgenus *Orthestheria (Migransia)* from the Tacuarembó Formation (Late Jurassic–?Early Cretaceous, Uruguay) with notes on its geological age

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In memoriam Ing. Lorenzo A. Ferrando (1943–2002)

Abstract

Conchostracans from the Tacuarembó Formation s.s. of Uruguay are reassigned to the subgenus *Orthestheria (Migransia)* Chen and Shen. They show more similarities to genera of Late Jurassic age in the Congo Basin and China than to those of Early Cretaceous age. On the basis of the character of the conchostracans, we suggest that the Tacuarembó Formation is unlikely to be older than Late Jurassic. It is probably Kimmeridgian, but an Early Cretaceous age cannot be excluded. This finding is consistent with isotopic dating of the overlying basalts, as well as the age range of recently described fossil freshwater sharks.

Keywords: Conchostracans; Late Jurassic; Tacuarembó Formation; Uruguay

Resumen

Los conchóstracos presentes en la Formación Tacuarembó s.s. (Uruguay) son reasignados al subgénero *Orthestheria (Migransia)* Chen and Shen. Estos muestran mayor similitud con los del Jurásico Tardío de la Cuenca del Congo y de China, que con géneros del Cretácico Temprano. De acuerdo a estas inferencias, la Formación Tacuarembó tendría una edad no más antigua que el Jurásico Tardío, perteneciendo probablemente al Kimmeridgiano; pero no puede ser descartada la posibilidad de una edad cretácica temprana. Estas conclusiones concuerdan con la información provista por dataciones de los basaltos suprayacentes a la Formación Tacuarembó y con el rango temporal de los tiburones de agua dulce recientemente descriptos.

Palabras clave: Conchóstracos; Formación Tacuarembó; Uruguay

1. Introduction

The conchostracan faunas of Uruguay, with few records of their presence in the fossil profile, are poorly understood. Herbst and Ferrando (1985) were the first to describe fossil conchostracans from the Tacuarembó Formation s.s. as *Cyzicus (Lioestheria) ferrandoi* Herbst (Cyzicidae) and propose a Late Triassic age for the lower member of the Tacuarembó Formation. Gallego et al. (1993) also describe *Cyzicus (Euestheria) falconeri* Gallego from the Upper Permian (Kazanian) Yaguarí Formation in northern Uruguay. More recently, Gallego et al. (1999) described two species, *Palaeolimnadiopsis hectori* Gallego (Palaeolimnadiopseidae) and *Tenuestheria canelonesensis* Gallego (Euestheriidae), and noted the probable presence of *Euestheria ?pricei* Cardoso (Euestheriidae) in the Early

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Fig. 1. Map showing the Uruguayan location of fossil conchostracans. Locality 1: km 396, route 5, Tacuarembó Department; locality 2: Batoví Dorado Hill, Rivera Departament.

Cretaceous (Albian) Castellanos Formation of the Santa Lucia Basin.

Using material that Rafael Herbst and Lorenzo Ferrando collected from two localities at different levels of the Tacuarembó Formation s.s. (Figs. 1 and 2), we provide new information about the area. On the basis of a new taxonomic scheme for conchostracans and comparisons with material from Africa and China, we reassign the material to the subgenus *Orthestheria (Migransia)* Chen and Shen (Shen, 2003). According to new paleontological evidence and stratigraphical interpretations, we propose that this formation is probably Late Jurassic in age, though we acknowledge that it may extend to the Early Cretaceous.

2. Stratigraphy and geological background

The Tacuarembó Formation has been correlated with the Botucatú Formation of Brazil (França et al., 1995). Both rock units crop out in the Paraná Basin, throughout which Triassic fluvial-lacustrine deposits are succeeded by sediments of a large desert that covered the basin and much of southwestern Gondwana. The Triassic rocks unconformably overlie continental Upper Permian rocks. By the end of the Jurassic, the break up of Gondwana was characterized by the extrusion of tholeiitic basalts in the Paraná Basin, which constitute the Serra Geral basalt (França et al., 1995)—in Uruguay, called the Arapey Formation (Bossi and Navarro, 1991).

The Tacuarembó Formation crops out mainly in a discontinuous north–south-trending belt in the Uruguayan Departments of Tacuarembó and Rivera. Two unnamed members have been distinguished within the Formation (Bossi et al., 1975; Sprechmann et al., 1981). In the lower member, subhorizontal stratification predominates, though small ripples, flaser, and cross-bedding stratification are locally present. Different lithologies alternate, mainly fine- and medium-grained sandstones, shales, siltstones, and mudstones (Fig. 2). The most common colors are red-yellowish (10YR 7/4, 6/6, 8/2, 8/6), brown-reddish (5R, 4/6, 7/4), and orange-reddish (10 R 6/6, 4/6) (Lavina et al., 1985). The lower fossiliferous member may have been deposited subaqueously; Lavina et al. (1985) suggest a braided river environment. The occurrence of the large, thick-shelled, unionid bivalve *Tacuaremboia caorsii* (Martínez et al., 1993) suggests high water energy (Martínez et al., 1993).

The upper unfossiliferous member is characterized by the presence of sandstones produced by the deposition of sand dunes in an arid environment. Tabular-planar to cuneiform-planar cross-bedding dominates, and foresets have an average angle of 21.2°.

Ferrando and Andreis (1986) removed what they designated the Cuchilla Ombú Formation from the bottom of the lower member, claiming an eolian origin. Subsequently, Ferrando et al. (1987) employed the name Tacuarembó for the strata of the (constrained) lower member and named the upper member the Rivera Formation. In this paper, we adopt this nomenclature and use Tacuarembó Formation s.s. to avoiding any misunderstanding. Fig. 3 summarizes the evolution of the stratigraphy of these units.

2.1. Palaeontology

The Tacuarembó Formation s.s. yields fossils mainly or exclusively restricted to freshwater and terrestrial environments, including unionoid bivalves (*Tacuaremboia caorsii* Martínez, Figueiras and Da Silva, *Diplodon batoviensis* Martínez and Figueiras, and *D. dasilvai* Martínez and Figueiras), gastropods, ostracods, conchostracans, osteichthyes, dipnoans (*Ceratodus*), crocodiles, freshwater sharks, and dinosaurs. Most of these are of little use in resolving the age of the formation. They are poorly preserved, which makes the precise identification of lower-rank taxa very difficult, and those that are classified adequately are highly endemic or have a long geological range. The age of the Formation has been estimated, until recently, solely on the basis of stratigraphic criteria, and no consensus exists in the published literature. For example,

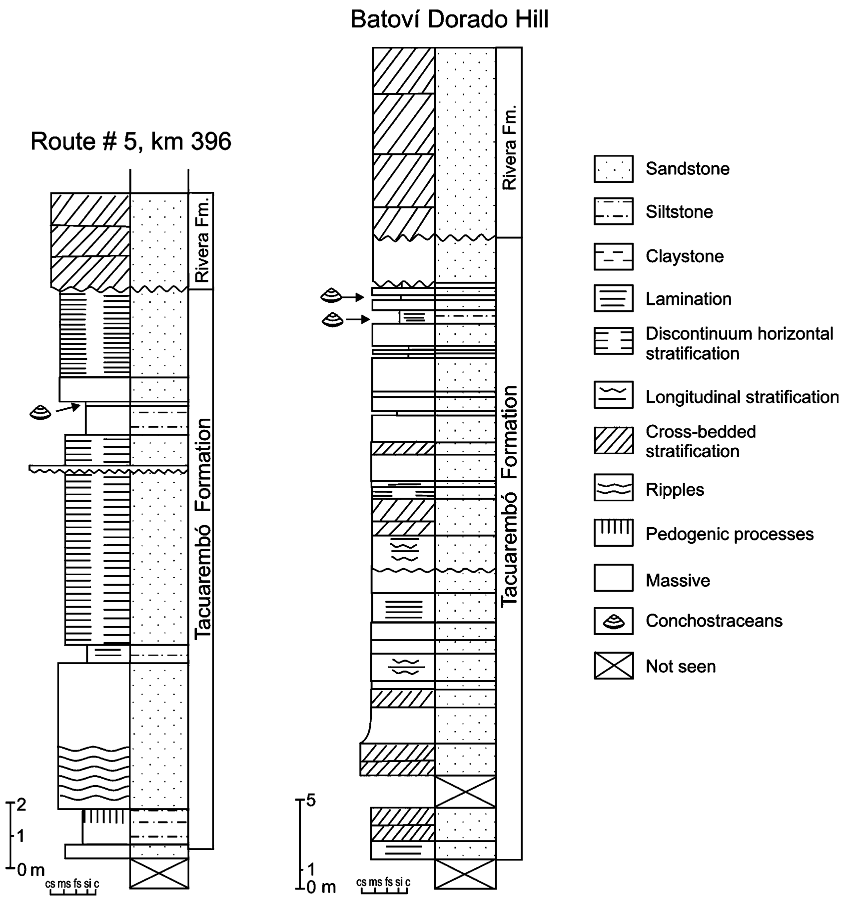

Fig. 2. Stratigraphic section showing location of beds containing fossiliferous samples and lithostratigraphic nomenclature applied to parts of the succession (modified from Herbst and Ferrando, 1985).

Sprechmann et al. (1981) and Martínez and Figueiras (1991) assign a late Triassic or Early Jurassic–Early Cretaceous age to it, whereas Herbst and Ferrando (1985) consider the lower member of the Tacuarembó Formation as Late Triassic and the upper member as Jurassic.

Recent progress in the identification of vertebrate material provides valuable evidence for the age. Perea et al. (2001 and references therein) identify theropod teeth similar to those of certain Coelurosauria, as well as the first non-African discovery of the freshwater hybodontid shark *Priohybodus* cf. *P. arambourgi* D'Erasmo, which is known only from the Upper Jurassic–Lower Cretaceous deposits in Saharan, Africa. The latter finding enabled them to propose an Upper Jurassic–?Lower Cretaceous age for the formation.

2.2. Isotopic dating

The Tacuarembó Formation s.s is comfortably overlain by the Rivera Formation, which is overlain by, and sometimes interbedded with, the Arapey Formation (Sprechmann et al., 1981; Bossi and Navarro, 1991). The Arapey Formation has been radiometrically dated at 126.8 ± 3.1 to 152.4 ± 8.2 Ma and 129.9 ± 1.1 to 132.9 ± 1.3 Ma by K/Ar and Ar/Ar, respectively (Creer et al., 1965; Féraud et al., 1999). Taking into account the radiometric dates, the stratigraphic relationships, and the known fossil record of *Priohybodus arambourgi* D'Erasmo, the Tacuarembó Formation cannot be older than Kimmeridgian or younger than Hauterivian (Perea et al., 2001).

<table>
<tr><th>Falconer, 1931</th><th colspan="2">Bossi et al., 1975</th><th colspan="2">Ferrando & Andreis, 1986</th><th>Ferrando et al., 1987</th></tr>
<tr><td rowspan="3">Areniscas de Tacuarembó (Tacuarembó Sandstones)</td><td rowspan="3">Tacuarembó Formation</td><td>upper member</td><td rowspan="2">Tacuarembó Formation</td><td>upper member</td><td>Rivera Formation</td></tr>
<tr><td rowspan="2">lower member</td><td>lower member</td><td>Tacuarembó Formation</td></tr>
<tr><td colspan="2">Cuchilla Ombú Formation</td><td>Cuchilla Ombú Formation</td></tr>
</table>

Fig. 3. Summary of the evolution of the stratigraphy of the Tacuarembó sandstones.

3. Systematic palaeontology

Order Conchostraca Sars, 1867
Surperfamily Estheriteoidea Zhang and Chen (Zhang et al., 1976)
Family Fushunograptidae Wang (in Hong et al., 1974)
Genus *Orthestheria* Chen (Zhang et al., 1976)
Subgenus *Migransia* (Chen and Shen) Shen, 2003
Orthestheria (Migransia) ferrandoi (Herbst), Shen and Gallego (Figs. 4 and 5a–f)
Cyzicus (Lioestheria) ferrandoi Herbst 1985 (in Herbst and Ferrando, 1985, Pl. 1, Figs. 1–10)

Diagnosis. Small shell, subcircular or elliptical in outline; short dorsal margin; growth bands ornamented with simply radial striae and growth lines with serrated structure.

Description. Carapace valve subcircular or elliptical in outline, small in size; dorsal margin short and slightly arched; anterior and posterior margins rounded; ventral margin slightly curved downward; growth bands ornamented with simply radial striae with fine cross-bars between striae, which form discontinuous striae in the external mold in the middle and upper parts of the valve; radial striae change to short and tuberculate sculpture on the ventral part

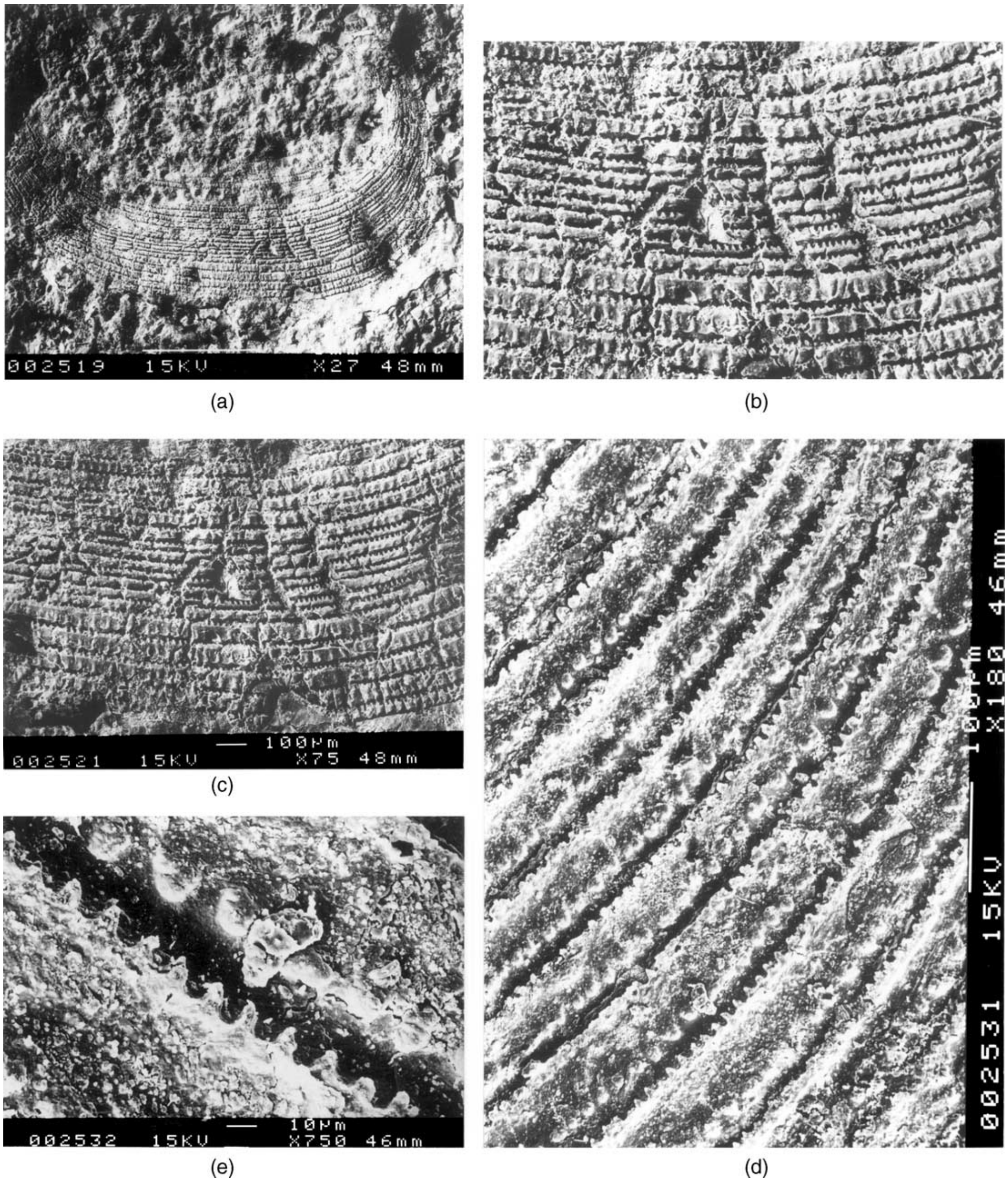

Fig. 4. *Orthestheria (Migransia) ferrandoi* (Herbst). (a) External mold of the right valve, ×27, No.10, Cat. No. 3641-1, Batoví Dorado Hill, Rivera area, Uruguay; (b, c) radial striae sculpture and beading structure on the postero-ventral part of the valve, ×75, ×50, same locality as a; (d, e) tubercular sculpture on the lower part of the growth bands and beading structure along the lower margin of the growth lines of the valve, ×180, ×750, No. 13, Cat. No. 3642, km 396 (Route 5), Tacuarembó area, Uruguay.

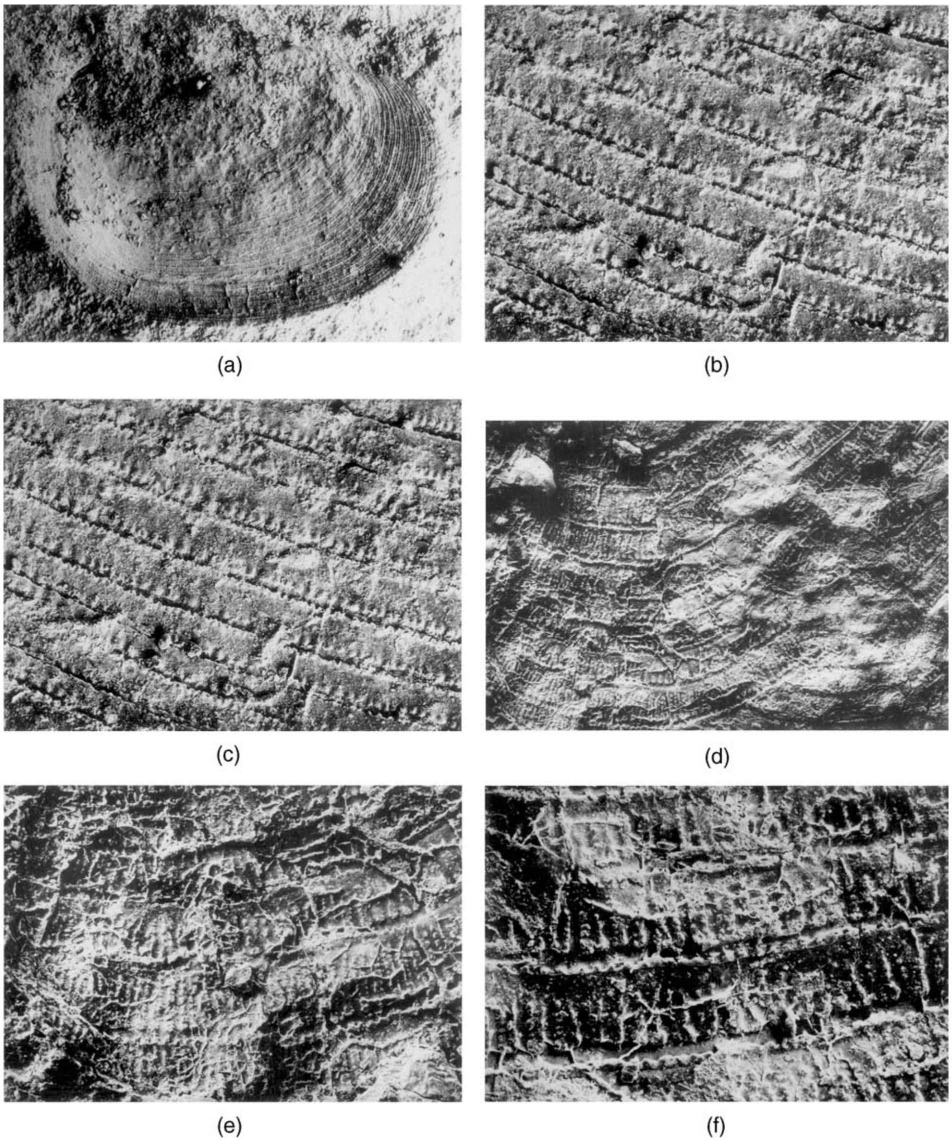

Fig. 5. *Orthestheria (Migransia) ferrandoi* (Herbst). (a) External mold of the right valve, × 12, No. 13, Cat. No. 3643, km 396 (Route 5), Tacuarembó area, Uruguay; (b) tubercular sculpture and beading structure near the ventral part of the valve, × 80, same locality as a; (c) external mold of the right valve, × 15.6, No. 12, Cat. No. 3644, Batoví Dorado Hill, Rivera area, Uruguay; (d, f) discontinuous radial striae sculpture and beading structure on the same part of the valve, × 50, × 100, × 180, association with No. 10 (see Fig. 3a), Cat. No. 3641-2.

of the valve; numerous growth lines with serrated structure along their lower margin.

Measurements. (in mm). L: 3.2–7.8; H: 2.1–6 (Herbst and Ferrando, 1985).

The samples studied here are archived by the Paleontology Department, Facultad de Ciencias Montevideo, Uruguay, with numbers 3641–3644. Supplementary material is held by the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. The samples studied by Herbst and Ferrando (1985) are kept in the paleozoological collection of the Facultad de Ciencias Exactas y Naturales y Agrimensura (Universidad Nacional de Nordeste, Corrientes, Argentina) under the collection number PZ-CTES. The holotype is PZ-CTES No. 5018 at locality km 396, route 5, Tacuarembó, Uruguay. The paratypes are PZ-CTES No. 5012, 5019, and 5028 (same locality as the holotype) and 5073 and 5075 from locality Batoví Dorado Hill, 23 km SE of Rivera, Uruguay. Additional material includes PZ-CTES No. 5011–5040 and 5053–5072.

Herbst and Ferrando (1985) assign these specimens to *Cyzicus (Lioestheria) ferrandoi* Herbst. Kozur et al. (1981) amend the genus *Lioestheria* to include species with a large umbo on which there is a longer node, though the interspaces are ornamented with a hachure-like sculpture. The growth lines are not beaded. Therefore, these specimens from Tacuarembó Formation s.s. should be assigned to the subgenus *Orthestheria (Migransia)*, which is characterized by a small valve, short dorsal margin, interspace ornamented with more regular radial striae, and growth lines with serrated lower margins (Chen and Shen, 1977).

All conchostracan specimens with beaded serrations along the growth lines have been considered examples of the Family Afrograptidae, which ranges from Early Triassic to Early Tertiary and includes approximately 22 genera (Chen and Shen, 1977, 1982; Shen and Chen, 1979; Chen and Hudson, 1991; Shen et al., 2002). As a result, the afrograptideans collectively include extremely variable ornamentation (e.g., reticulations, radial striae, dendritic striae, foveolae) and valve structures and, therefore, are a complex group.

However, the serrated structure (setose armature or subtle setae) of the growth lines exists in living species in three of the five extant conchostracan families (Lynceidae, Cyzicidae, and Leptestheriidae) (Shen et al., 2002; Shen, 2003). For example, Sars (1896, p. 23) observed that in *Caenestheria packardi* (Brady) (= *Estheria packardi*), "the setous armature of the lines of growth and of the free edges of the valve could be discerned, but the bristles gradually become shorter and partly broken off, so as at least, for the most part, only to leave their insertions." Thus, the insertions had formed a serration margin along the growth lines of fossil conchostracans. Judging from this, the serration structure is not the only important character for the Family Afrograptidae (Shen et al., 2002). Therefore, we assign *O. (Migransia) ferrandoi* (Herbst) nov. comb. to the Family Fushunograptidae on the basis of its interspaces with radial striae sculpture (Shen, 2003).

Herbst and Ferrando (1985) describe two different populations of *O. (Migransia) ferrandoi* (Herbst) from Batoví Dorado Hill and km 396 localities, distinguished by the size of the carapace. The specimens from km 396 locality are slightly larger than those from the Batoví Dorado Hill. These differences may be due to environmental conditions, the presence of different ontogenetic stages, sexual dimorphism, or a combination thereof (Herbst and Ferrando, 1985). In any case, the different sizes do not indicate that this species should be split into two different species.

Cyzicus? *codoensis* Cardoso, from the Lower Cretaceous Lagarcito Formation of Argentina (Chiappe et al., 1998), resembles *Orthestheria (Migransia)* in terms of its beaded structure and hachure-type marking on the growth bands. However, the taxonomic position of the former is now reassigned as a new species of the genus *Dendrostracus* (Chen and Hudson, 1991) on the basis of the dendritic ornamentation between growth lines.

4. Conchostracan relationships among South America, Africa, and China

According to its shell configuration, ornamentation, and the presence of a serrated margin, *O. (Migransia) ferrandoi* (Herbst) is very close to *O. (Migransia) biaroensis* and *O. (Migransia) caheni* (Defretin-Lefranc) (Defretin-LeFranc, 1967, Pl. 5, Figs. 4–8 and Pl. 8, Figs. 1–5). Both of the latter occur in the Stanleyville Series of the north Congo Basin (Big. 6), which is considered Late Jurassic (Kimmeridgian) in age. *Orthestheria (Migransia) ferrandoi* (Herbst) is distinguished by the presence of tubercular sculpture on the interspaces (Figs. 4d, e and 5b). *O. (Migransia) ferrandoi* (Herbst) also resembles *O. (Migransia) kasaiensis* (Marlière) from the Loïa Series (Wealden) of the north Congo Basin, which possesses an oval configuration and more regular radial striae on the growth bands (Defretin-LeFranc, 1967, Pl.4, Figs. 1–4).

In China, *O. (Migransia)* first appears in the Late Jurassic (Kimmeridgian) and diversifies in the Early Cretaceous (Barriasian-Barremian). *O. (Migransia) ferrandoi* (Herbst) resembles samples from the Late Jurassic more than those from the Early Cretaceous due to its discontinuous radial striae, such as *O. (Migransia) sichuanensis* from the Upper Jurassic Penglaizhen Formation of Sichuan Province, SW China (Shen and Chen, 1982, Pl. 9, Figs. 1–3), and *Qinghaiestheria hungshuikouensis* from the Upper Jurassic Hungshuikou Formation of Qinghai Province, NW China (Chang, 1957; Wang, 1983) (Fig. 6). Both species are associated with an ostracod *Cetacella–Djungarica–Damonella* fauna and an unionoid bivalve *Danlengiconcha* assemblage, which has Tethyan biogeographical affinity (Liu, 1982; Cao, 1999). *Cetacella* is one of the most important components of the Late Jurassic ostracod fauna, particularly in the Kimmeridgian of Europe (Helmdach, 1971; Ainsworth et al., 1989). It also occurs in the Morrison Formation (Kimmeridgian) of Colorado and Oklahoma, USA (Schudack et al., 1998). The bivalve *Danlengiconcha* is an endemic element that ranges from the late Middle Jurassic to early Early Cretaceous, but it flourished in the Late Jurassic, especially the Kimmeridgian, and spread southwest and northwest in China along the margin of the Tethys Sea (Liu, 1982).

Several conchostracan taxa from the Hungshuikou Formation, with the exception of *Qinghaiestheria hungshuikouensis* (Chang), resemble those of the Stanleyville Series. *Sinoestheria tsaidamensis* (Chang), for example, resembles *Paleolimnadiopsis lombardi* (Defretin-LeFranc), in that is possesses large valves, large polygonal reticulations, and stout growth lines with a row of large round nodes (Chang, 1957; Chen and Shen, 1982). The conchostracans of the Tacuarembó Formation s.s, therefore, show more similarities to those of the Late Jurassic in the Congo Basin and China than to those of Early Cretaceous age. In turn, we suggest that this formation is not older than Late Jurassic, and possibly of Late Jurassic (probably Kimmeridgian) age, though the possibility that it extended into the Early Cretaceous cannot be excluded. This is consistent with isotopic dating and fossil freshwater sharks.

East Gondwanaland separated from Africa and South America during the Early Jurassic. During the Early

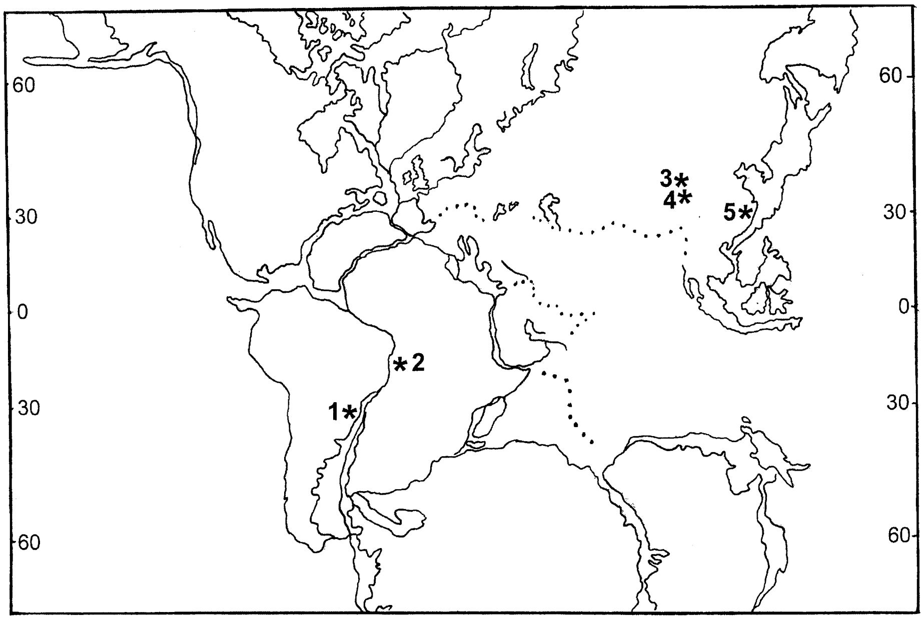

Fig. 6. Distribution of *Orthestheria (Migransia)* in the paleocontinental blocks during the Late Jurassic and Early Cretaceous. (1) Tacuarembó Formation (Late Jurassic–?Early Cretaceous), Tacuarembó-Rivera area, Uruguay; (2) Stanleyville (Kimmeridgian) and Loïa (Wealden) series, Congo Basin; (3) Hungshuikou Formation (Kimmeridgian), Qianhai, NW China; (4) Penglaizhen Formation (Kimmeridgian), Sichuan Province, SW China; (5) Lower Cretaceous Shouchang Formation, Zhejiang Province, SE China (modified from Smith and Briden, 1977, Map 9; Tithonian).

Cretaceous (Valanginian), South America separated from Africa (Norton, 1982). The conchostracan *O. (Migransia)* and the freshwater sharks of the Tacuarembó Formation show a close relationship with Africa and may belong to the same paleobiogeographic province. Some conchostracan genera from China are similar to those from the Late Jurassic and Cretaceous of Africa, though other groups, such as bivalves and ostracods associated with the conchostracans, indicate a Tethys biogeographical province. The close relationship between the northern and southern continental blocks may support parallel evolution in the fossil conchostracan fauna following origination from a common ancestor.

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