The halobiid bivalve genus *Enteropleura* and a new species from the Middle Anisian of Guangxi, southern China

JIN-HUA CHEN and FRANK STILLER

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Enteropleura is a short-ranged early Middle Triassic bivalve genus, of importance with regard to biostratigraphy and the phylogeny of the Halobiidae. It comprises five species from the Alps, the Dinarides, Nevada, and southwestern China. *Enteropleura walleri* sp. nov. from the Fengshan District, northwestern Guangxi, southwestern China, occurs in the central area of the Triassic Nanpanjiang Basin. The new species is of late Middle Anisian age, penecontemporaneous to the species from Europe and Nevada. Morphologically, *E. walleri* sp. nov. is similar to *Enteropleura jenksi* from Nevada, *Enteropleura bittneri* from Austria, and *Enteropleura lamellosa* from Croatia, but it differs significantly from *Enteropleura guembeli* from Hungary. Two species-groups of *Enteropleura* thus may be differentiated, *E. guembeli* group and *E. bittneri* group. Re-examination of *E. guembeli* reported from the Anisian basin slope facies in Guizhou, southwestern China, confirms its taxonomic status.

Key words: Bivalvia, Halobiidae, *Enteropleura*, Triassic, Anisian, Guangxi, China.

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Introduction

The short-ranged early Middle Triassic genus *Enteropleura* Kittl, 1912 comprises thin-shelled bivalves that are fairly similar to *Daonella* Mojsisovics, 1874. The genus was erected by Kittl (1912), based on *Daonella guembeli* Mojsisovics, 1874 from the *Balatonites* Beds of western Hungary and "*Posidonomya* nov. spec." of Arthaber (1896) from the Rahnbauerkogel fauna in Großreifling, Austria. Kittl (1912) regarded an internal ridge to be characteristic of *Enteropleura* and distinguishing it from *Daonella*. Since then, the genus has been of considerable interest to palaeontologists (e.g., Krumbeck 1924; Ichikawa 1958; Cox 1969; De Capoa Bonardi 1970; Campbell 1994; McRoberts 2000). However, the genus was poorly known, because only few fossils from a very limited number of localities had been described. Only few studies mentioned the genus *Enteropleura* from China, and until now it is known from very few Chinese localities. The stratigraphical range of the genus has long been misunderstood (e.g., Yin 1985; Chen 2004).

Recently, Waller and Stanley (2005) and Hopkin and McRoberts (2005) reported new, well-preserved specimens of *Enteropleura* from Nevada, and Waller (in Waller and Stanley 2005) discussed the genus in detail. They recognised three species, two in the Alps [*Enteropleura guembeli* (Mojsisovics, 1874), *Enteropleura bittneri* Kittl, 1912] and one in Nevada [*Enteropleura jenksi* Hopkin and McRoberts, 2005 (= *Enteropleura* species *a* of Waller in Waller and Stanley 2005)]. Based on the correlation of Bucher (1992), Waller and Stanley (2005) concluded that these three species are limited to a narrow stratigraphical interval, the *Balatonites shoshonensis* Zone (late Middle Anisian). Herein, the genus *Enteropleura* is re-evaluated, and besides the three species mentioned above and the new species described below, *Daonella lamellosa* Kittl, 1912 from the Anisian of the Dinarides of Dalmatia, Croatia, is assigned to *Enteropleura*.

Due to the complicated tectonical setting, the Middle Triassic stratigraphy in northwestern Guangxi was poorly known before 1980. Recent investigations resulted in a rough stratigraphical sequence of the Triassic (Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region 1985). Gu et al. (1976) and Gan (1983) reported several species of *Daonella* from the Middle Triassic of this region. Chen et al. (1992) suggested a *Daonella* succession for northwestern Guangxi, ranging from the Upper Anisian to the top of the Ladinian, and described the index species for five *Daonella* zones. Reporting a new bivalve from the Lower Anisian of northwestern Guangxi, Chen and Komatsu (2002) provided a reconstruction of the palaeogeography in the Nanpanjiang area. In addition, they mentioned the occurrence of *Enteropleura* sp. (sp. nov.?) in the Middle Anisian of Guangxi. In the present contribution, this new taxon is described as *Enteropleura walleri* sp. nov.

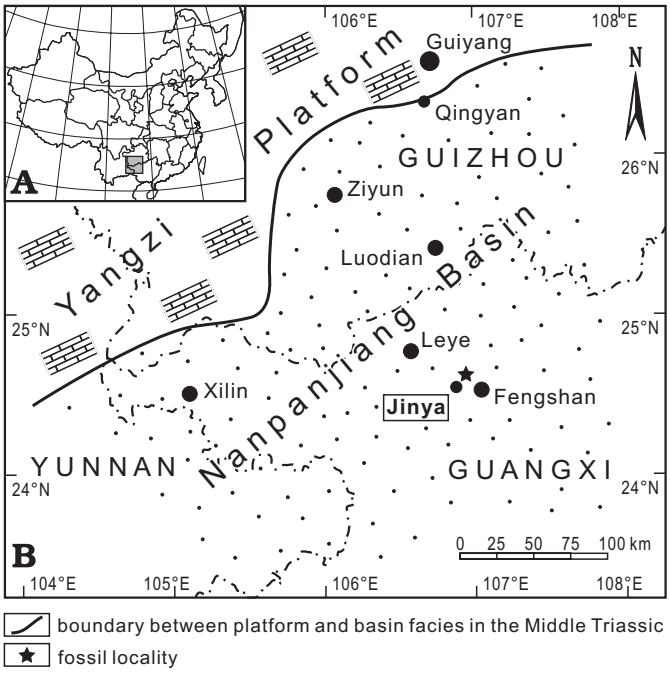

Fig. 1. Location of the fossil site near Jinya in Fengshan District, northwestern Guangxi, southwestern China. **A**. General map of China with the area of map B marked. **B**. Map of northwestern Guangxi and southwestern Guizhou with location of the fossil site and reconstructed Anisian (Middle Triassic) palaeogeography (palaeogeographical reconstruction after Chen and Komatsu 2002).

The new species *Enteropleura walleri* from Jinya, Fengshan District, northwestern Guangxi, southwestern China (Fig. 1), is known from a monospecific assemblage of late Middle Anisian age occurring in the central area of the Triassic Nanpanjiang Basin, in the upper part of the Lower Member of the Banna Formation (Fig. 2). *Enteropleura walleri* thus is penecontemporaneous to the *Enteropleura* species in Europe and Nevada.

Previously, a single species of *Enteropleura* was reported from China. *Enteropleura guembeli* (Mojsisovics, 1874) was described from the basin slope facies of the lower part of the Anisian Xinyuan Formation in Ziyun District, southwestern Guizhou (Chen et al. 1974; Gu et al. 1976; Gan and Yin 1978) (Fig. 1). Herein, the specimen figured in these Chinese publications is re-described for comparison.

Institutional abbreviations.—NIGP, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Geological setting

The Middle Triassic strata in Fengshan District generally are made up of the Banna Formation (Anisian) and the Lanmu Formation (Ladinian). These two formations are correlated with the Xinyuan Formation and the Bianyang Formation of the Ziyun-Luodian area, southwestern Guizhou, respectively (Fig. 2). The Anisian Banna Formation is disconformably underlain by the limestones of the Early Triassic Luolou Formation (Fig. 3).

The Late Anisian and Ladinian rocks of the Fengshan District are composed of turbidites (sandstones and siltstones) with a total thickness of more than 3000 m. The strata are considered to have been deposited in basin slope environments (Gan 1983; Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region 1985; Guizhou Bureau of Geology and Mineral Resources 1987; Chen et al. 1992). The Early and Middle Anisian deposits of the Fengshan District, i.e., the Lower Member of the Banna Formation, are only about 45–60 m thick and characterised by finely laminated shales/mudstones and limestones (Fig. 3). During the Early and Middle Anisian, the Fengshan District was located in the central area of the Nanpanjiang Basin (Fig. 1) (Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region 1985; Regional Geological Surveying Team of Guizhou Bureau of Geology and Mineral Resources 1992; Chen et al. 1992; Chen and Komatsu 2002).

The specimens of *Enteropleura walleri* sp. nov. come from the upper part of the Lower Member of the Banna Formation. Herein, the Lower Member of the Banna Formation is subdivided into five stratigraphical units, lettered A to E in ascending order (Figs. 2, 3).

Unit A is 4.8 m thick and consists of grey, thinly-bedded limestones with few intercalations of black, thinly-bedded calcareous mudstones. This unit rarely yields specimens of the bivalve *Periclaraia jinyaensis*. Ammonoids of the genera *Japonites*, *Leiophyllites*, and *Hollandites* are abundant. At the Shipao section, Unit A yields conodonts of the genera *Fragmenis*, *Neospathodus*, *Enatiognathus*, *Pollognathus*, *Prioniodina*, *Hindeodella*, *Cypridodella*, *Neohindeodella*, and *Gladigondolella*.

Unit B is an alternation of black calcareous mudstones and marls, about 11 m thick. It yields the bivalves *Periclaraia*

<table>
<tr><td colspan="2" rowspan="2">Age</td><td colspan="5">NW Guangxi
(after Chen et al. 1992; modified)</td><td rowspan="2">SW Guizhou
(Gan 1983)</td></tr>
<tr><td colspan="2">Xilin - Leye</td><td colspan="3">Fengshan</td></tr>
<tr><td rowspan="3">Ladinian</td><td>Late</td><td rowspan="3">Hekou Fm.</td><td>Mb. 3</td><td rowspan="3">Lanmu Fm.</td><td>Third Mb.</td><td rowspan="3">Bianyang Formation</td></tr>
<tr><td>Mb. 2</td><td>Second Mb.</td></tr>
<tr><td>Early</td><td>Mb. 1</td><td>First Mb.</td></tr>
<tr><td rowspan="5">Anisian</td><td>Late</td><td rowspan="5">Baifeng Fm.</td><td>Mb. 4</td><td rowspan="5">Banna Fm.</td><td>Upper Mb.</td><td rowspan="5">Xinyuan Formation</td></tr>
<tr><td rowspan="3">Middle</td><td rowspan="2">Mb. 3</td><td rowspan="4">Lower Mb.</td><td>E</td></tr>
<tr><td>D</td></tr>
<tr><td>Mb. 2</td><td>C</td></tr>
<tr><td>Early</td><td>Mb. 1</td><td>B</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>A</td><td></td></tr>
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Fig. 2. Stratigraphical subdivision and correlation of the Middle Triassic in northwestern Guangxi and southwestern Guizhou, southwestern China (Fm., Formation; Mb., Member) (not to scale with regard to unit thicknesses).

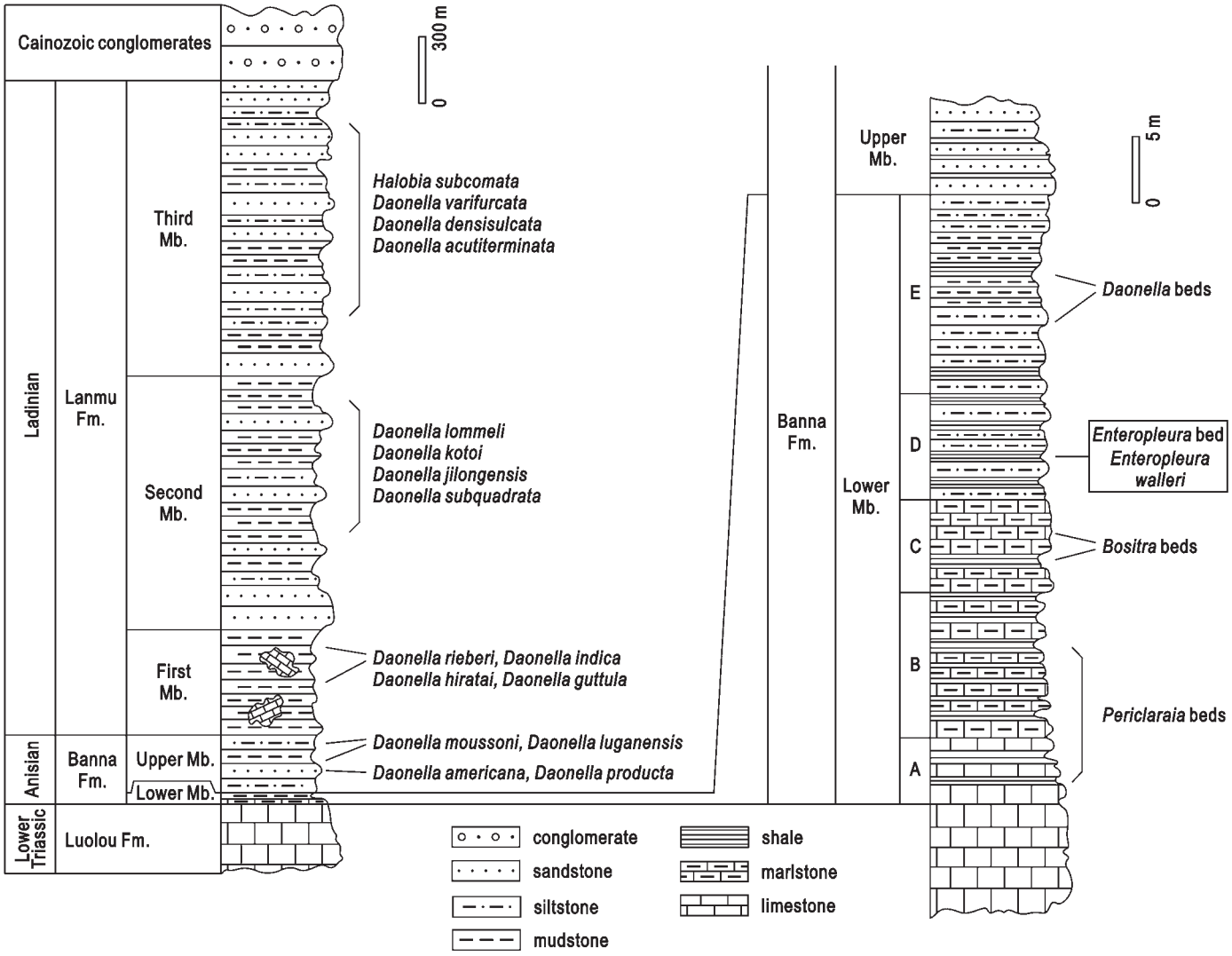


Fig. 3. Columnar stratigraphical and lithological section of the Middle Triassic in the Fengshan District, Guangxi, and the occurrences of bivalves, especially showing the Early and Middle Anisian Lower Member of the Banna Formation (Fm., Formation; Mb., Member); taxonomic identifications of the bivalves in the Upper Anisian and Ladinian by Chen et al. (1992).

jinyaensis and *Bositra* sp. as well as ammonoids of the genera *Hollandites*, *Acrochordiceras*, *Paracrochordiceras*, *Balatonites*, and *Japonites*. Bivalves of some other genera such as *Leptochondria*, *Praechlamys*, and *Ornithopecten* were found in horizons of the Leye section equivalent to Unit A and Unit B. The conodonts and ammonoids of the units A and B indicate an Early Anisian age.

Unit C is 7 m thick and characterised by black or grey marls, with occasional intercalations of calcareous mudstones. This unit yields bivalves of the genus *Bositra* as well as ammonoids of the genera *Beyrichites*, *Hollandites*, *Acrochordiceras*, and *Balatonites*. The specimens of *Bositra* are morphologically close to *Bositra favretensis* described from the *Acrochordiceras hyatti* Zone (early Middle Anisian) of Nevada (Waller and Stanley 2005).

Unit D mainly is an alternation of grey siltstones and mudstones, 8 m thick. *Enteropleura walleri* sp. nov. abundantly occurs in a grey silty mudstone of about 1 m thickness in the middle part of this unit. The ammonoids "*Paraceratites*" cf. *binodosus*, *Balatonites* cf. *balatonicus*, and *Gymnites* sp. occur in the upper part of the unit and are correlated with the *Balatonites balatonicus* Zone or the Pelsonian substage of Alpine Europe (Chen et al. 1992). The Pelsonian substage may be correlated with the late Middle Anisian *Balatonites shoshonensis* Zone of Nevada (Silberling and Nichols 1982; Bucher 1992).

Unit E consists of an alternation of mudstones and siltstones, with a total thickness of 15 m. Its lower part is composed of grey and brown mudstones intercalated with siltstones, and its upper part mainly of siltstones. The ammonoid genera *Balatonites* and *Gymnites* as well as the bivalve genus *Daonella* occur in the lower part of the unit, about 10 m below the upper boundary of Unit E. The Upper Member of the Banna Formation conformably overlays Unit E and yields *Daonella americana* in its lower part (Chen et al. 1992). *Daonella americana* is the characteristic species of the *Gym-*

notoceras rotelliformis Zone (early Late Anisian) in Nevada (Silberling and Nichols 1982: 67). Therefore, the age of Unit E most probably is latest Middle Anisian. The specimens of the genus *Daonella* in Unit E indicate the first appearance of this genus in Guangxi.

Taphonomic observations

The specimens of *Enteropleura walleri* sp. nov. are preserved in a grey, thinly-bedded, silty mudstone. The shell substance has been completely dissolved during diagenesis, and the bivalves are preserved in the form of internal and external moulds, often as composite moulds. These "flat clams" generally occur in high abundances in typical monospecific assemblages on bedding planes, sometimes associated with few ammonoids. Articulated valves are abundant, and they commonly are preserved in an open position (butterfly position). There are no indications of abrasion or breakage, even though the valves were extremely thin. This mode of occurrence suggests that the assemblages are parautochthonous.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758
Subclass Autolamellibranchiata Grobben, 1894
Superorder Pteriomorphia Beurlen, 1944
Order Pterioida Newell, 1965
Suborder Pterioidina Newell, 1965
Superfamily Posidonioidea Frech, 1909
Family Halobiidae Kittl, 1912

Diagnosis (after Waller in Waller and Stanley 2005: 21).—Monomyarian Posidonioidea with broadly expanded shells of low convexity, hinge long, commonly nearly as long as shell length, ligament alivincular or horizontally striated, commarginal plicae limited to early ontogeny, radial costellae, if present, stronger than commarginal ornament in late ontogeny.

Genus *Enteropleura* Kittl, 1912

Type species: *Daonella guembeli* Mojsisovics, 1874 (subsequent designation by Diener 1923: 52); Middle Anisian (Middle Triassic), western Hungary.

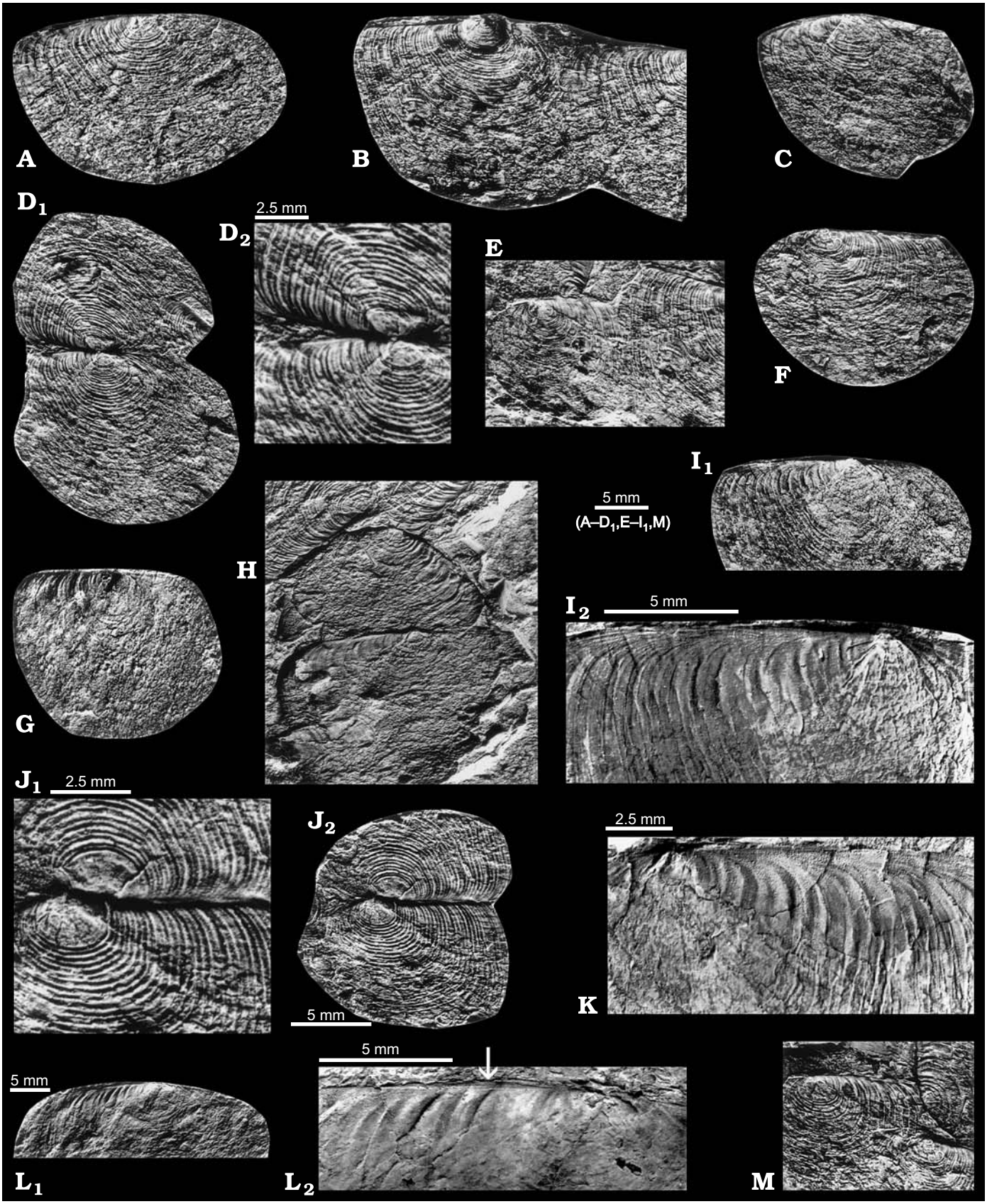
Species included: *Enteropleura bittneri* Kittl, 1912; *Enteropleura lamellosa* (Kittl, 1912); *Enteropleura jenksi* Hopkin and McRoberts, 2005; *Enteropleura walleri* sp. nov.

Diagnosis (after Waller in Waller and Stanley 2005: 21).—Halobiidae with an alivincular ligament, hinge shorter than shell length, and ornamentation that is intermediate between that of *Bositra* and *Daonella*.

Discussion.—Kittl (1912) regarded the internal shell ridges as an important character of *Enteropleura* Kittl, 1912, distinguishing it from *Daonella* Mojsisovics, 1874. However, Krumbeck (1924) showed that the internal ridges described by Kittl (1912) are also present in both *Daonella* and *Halobia* Bronn, 1830, and therefore regarded the genus name *Enteropleura* as invalid. Campbell (1994: 44), following Krumbeck (1924), regarded the internal ridges as growth tracks of the adductor muscle scar. Ichikawa (1958: 190) included *Enteropleura* as a subgenus in *Daonella*. McRoberts (2000: 600) considered *Enteropleura* as a separate genus but "poorly known", which "may, after further study, be placed in the Halobiidae". Waller and Stanley (2005) and Hopkin and McRoberts (2005) recognised *Enteropleura* as being a valid genus within the Halobiidae. Waller (in Waller and Stanley 2005) further pointed out that *Enteropleura* has an alivincular ligament, which was first reported by Arthaber (1896: 194, fig. 12) in "*Posidonomya* nov. spec." (= *Enteropleura bittneri*).

The commarginal sculpture in *Enteropleura* is usually fine and regular (except for *Enteropleura guembeli*), and the radial sculpture, if present, is fine and weak. This shell sculpture differs from that in most species of *Daonella*, in which the radial ribs are strong and the commarginal lirae are weak in late ontogeny. However, the radial sculpture is weak in some early species of *Daonella*, e.g., *Daonella boeckhi* Mojsisovics, 1874, possibly indicating an intermediate position between *Enteropleura* and *Daonella*. The alivincular ligament and the sculpture of *Enteropleura* are very similar to those of *Bositra* De Gregorio, 1886. But *Bositra* is relatively rounded or oval in shape, its hinge line is generally much shorter than the shell length, the auricles are very small or lacking, and the commarginal lirae are generally broader than those of *Enteropleura*. *Enteropleura* is closely related to both *Bositra* and *Daonella* and probably has phylogenetic relationships with these two genera. We agree with Waller (in Waller and Stanley 2005: 17, fig. 5) that *Enteropleura* probably is derived from a species of *Bositra* and evolved into early *Daonella* in the Middle Triassic.

Fig. 4. Halobiid bivalve *Enteropleura walleri* sp. nov. from Unit D of the Lower Member of the Banna Formation (late Middle Anisian, Middle Triassic), Jinya, Fengshan District, northwestern Guangxi, southwestern China. **A**. Internal mould, right valve, holotype, NIGP 140170. **B**. Internal mould, right valve, paratype, NIGP 140171. **C**. Internal mould, right valve, with clearly discernible indications of the internal posterior radial ridges, paratype, NIGP 140176; sculptural variant with commarginals on the anterior and central sectors very weak. **D**. Internal moulds, open-articulated specimen (right valve below, left valve above), with clearly discernible indications of the internal posterior radial ridges, paratype, NIGP 140177; D_2, dorsal valve parts with radial grooves (impressions of the internal radial ridges). **E**. Internal moulds, crowded valves, paratype, NIGP 140172. **F**. Internal mould, left valve, paratype, NIGP 140173. **G**. External mould, left valve, paratype, NIGP 140178; sculptural variant with commarginals on the anterior and central sectors very weak, nearly lacking. **H**. Internal moulds, crowded valves, paratype, NIGP 140174; sculptural variations: the commarginal lirae on the anterior and central sectors of the two valves in the middle and lower part are very weak, those of other valves (top left) are distinct. **I**. Internal mould, dorsal part of right valve, paratype, NIGP 140179; I_2, posterodorsal part, showing the commarginal undulations on the posterior sector and their branching into lirae ventrally. **J**. Internal moulds, open-articulated specimen, juvenile shell (left valve below, right valve above), with clearly discernible indications of the internal posterior radial ridges, paratype, NIGP 140182; J_1, dorsal →



valve parts with radial grooves (impressions of the internal radial ridges). **K**. Internal mould, posterodorsal part of left valve, paratype, NIGP 140180; showing the commarginal undulations on the posterior sector and their branching into lirae ventrally. **L**. Internal mould, dorsal part of right valve, paratype, NIGP 140181; L_2, posterodorsal part with narrow posterior auricle (arrow). **M**. Internal moulds, crowded valves, paratype, NIGP 140175.

Based on morphological characters, the five *Enteropleura* species may be subdivided into the following two species-groups. The character of the morphological differences, however, does not justify the formal erection of new subgenera.

The *Enteropleura guembeli* group comprises only *E. guembeli* (Mojsisovics, 1874), originally described from the *Balatonites* Beds (= *Balatonites balatonicus* Zone) of western Hungary. Characteristic features are a small size (usually 10–15 mm or less in length), a subcircular to suboval shell shape, and a sculpture of irregular commarginal rugae and very weak radial striae, lacking the fine, regular commarginal lirae that are characteristic for the species of the *Enteropleura bittneri* group.

The species of the *Enteropleura bittneri* group differ in the larger shell size (maximum length about 30 mm), the D-shape or *Daonella* shape, and the fairly regular sculpture of fine commarginal lirae and in most species additionally developed weak radial ribs. The shell surface usually can be subdivided into three contiguous radial sectors (triangular fields), which are differently sculptured. A small and very narrow posterior auricle is present. The group comprises the four species *Enteropleura bittneri* Kittl, 1912 from the Rahnbauerkogel fauna (*Balatonites balatonicus* Zone) of Großreifling, Austria, *Enteropleura lamellosa* (Kittl, 1912) from the Anisian of the Dinarides in Dalmatia, Croatia, *Enteropleura jenksi* Hopkin and McRoberts, 2005 from the *Balatonites shoshonensis* Zone, Favret Formation, Nevada, and *Enteropleura walleri* sp. nov. from Unit D (late Middle Anisian) of the Lower Member of the Banna Formation, Fengshan District, northwestern Guangxi.

Enteropleura bittneri and *E. jenksi* share the fine cancellate sculpture consisting of commarginal lirae and radial costellae, but the posterodorsal sector of *E. jenksi* is wider than that of *E. bittneri*, and the two species further differ in details of the beak and the shell outline. *Enteropleura lamellosa* is very similar to *E. bittneri* and *E. jenksi* in size, outline, and shell sculpture. However, in comparison to the latter two species, the commarginal lirae of *E. lamellosa* are slightly broader, the interspaces between the lirae are narrower, and the radial costellae appear weaker developed (fide the figures of Kittl 1912: pl. 10: 23, 24). With regard to general shell outline, *Enteropleura lamellosa* is similar to both *Daonella* and *Enteropleura*. Kittl (1912) assigned it to *Daonella* rather than to *Enteropleura*, because he could not observe the internal ridges. However, the presence or absence of the internal ridges is not significant for the distinction of *Enteropleura* from *Daonella* (Waller in Waller and Stanley 2005). The shell shape, hinge margin, and especially the shell sculpture of *E. lamellosa*, which consists of fine, regularly and closely spaced radials and commarginals, are much more similar to *Enteropleura* than to *Daonella*.

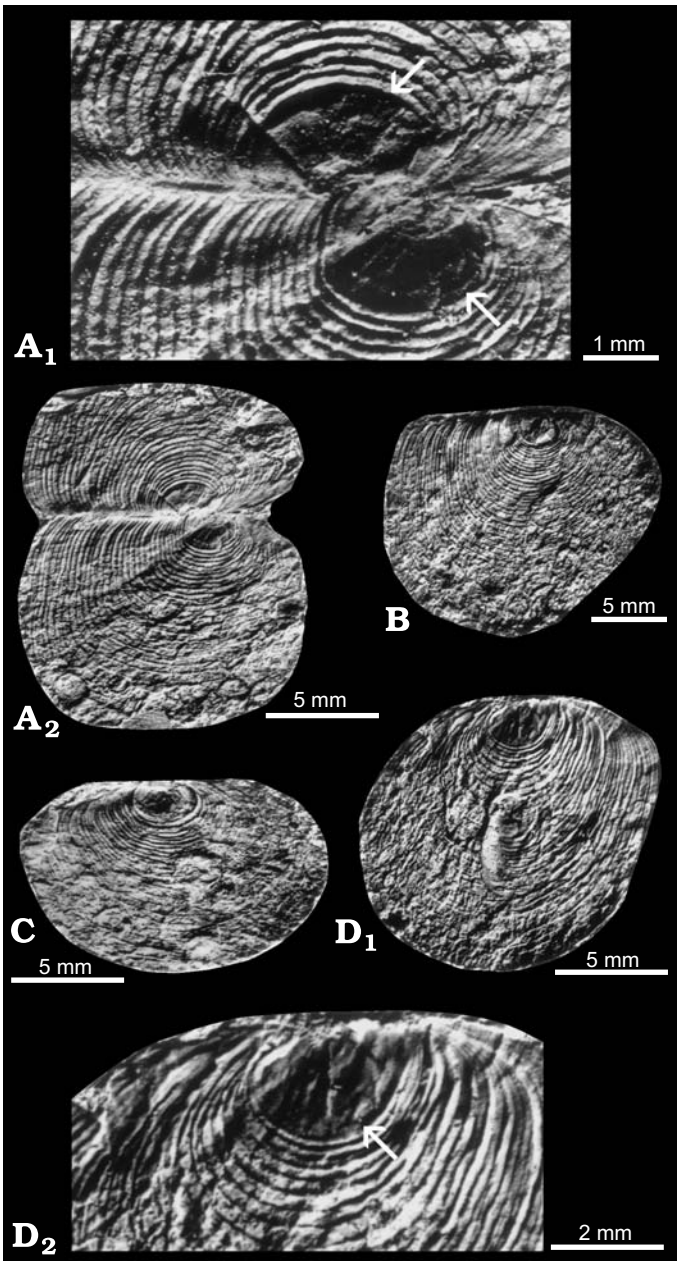


Fig. 5. Prodissoconch and juvenile shell morphology of the halobiid bivalve *Enteropleura walleri* sp. nov. from Unit D of the Lower Member of the Banna Formation (late Middle Anisian, Middle Triassic), Jinya, Fengshan District, northwestern Guangxi, southwestern China. **A**. External mould, open-articulated specimen (left valve below, right valve above), with clearly discernible indications of the internal posterior radial ridges, paratype, NIGP 140183; A_1, dorsal valve parts, arrows point to the margins of the prodissoconchs. **B**. External mould, left valve, paratype, NIGP 140184. **C**. External mould, right valve, paratype, NIGP 140185. **D**. External mould, left valve, with clearly discernible indications of the internal posterior radial ridges, paratype, NIGP 140186; D_2, dorsal valve part, arrow points to the margin of the prodissoconch.

Enteropleura walleri sp. nov.

Figs. 4, 5.

2002 *Enteropleura* sp. (sp. nov.?); Chen and Komatsu 2002: 436.

Derivation of the name: In honour to Thomas R. Waller, who has made important contributions to the research on Mesozoic bivalves.

Holotype: NIGP 140170 (Fig. 4A); right valve of an adult individual.

Paratypes: NIGP 140171–140186 (Figs. 4B–O, 5).

Type locality: Jinya, Fengshan District, northwestern Guangxi, southwestern China.

Type horizon: Middle part of Unit D of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic).

Material.—More than 100 external and internal moulds of right and left valves as well as numerous fragments from the same locality and horizon as the type specimens.

Measurements.—The holotype is 25.5 mm long and 16.0 mm high.

Diagnosis.—*Enteropleura* of medium size with a large prodissoconch and fine, regular commarginal sculpture; no radial sculpture. Differs from all other congeneric species in the lack of radial shell sculpture.

Description.—Shell of medium size, usually 20–25 mm (up to 30 mm) in length, D-shaped, longer than high (height/length ratio 0.62–0.82), nearly flat. Beak orthogyrous or slightly prosogyrous, projecting slightly above the dorsal margin, positioned anterior to mid-length. Hinge line short, about one-third to two-fifth of the shell length. Anterodorsal and posterodorsal margins nearly straight, descending very slightly from the beak; ventral margin broadly curved; anterior margin stronger curved and passing tangentially into the hinge margin; posterior margin almost straight, sharply curved posterodorsally and passing tangentially into the posterodorsal margin. Relative longitudinal elongation of the shell, relative length of the hinge margin, and relative position of the beak fairly variable, resulting in variable shell outlines (cf. Figs. 4, 5); however, besides intraspecific variability, diagenetical deformation may also partly be responsible for these variable shapes. Anterior auricle absent; posterior auricle small and very narrow (5–6 mm long, 0.2–0.3 mm high), separated from the disk by a narrow sulcus (Fig. 4L_2); posterior margin of auricle forming a very obtuse angle with its dorsal margin, angle subtended by the dorsal margin and the base of the auricle about 5–10°. Prodissoconch large, up to 2.8 mm in length, suboval, with comparatively indistinct, weak commarginal growth sculpture or almost smooth (Fig. 5). Posterior radial grooves (indicating the internal ridges anteriorly and posteriorly bordering the track of the ontogenetically migrating posterior adductor muscle scar) narrow and shallow (Figs. 4C, D, J, 5A, D); posterior groove generally present, 2.5–6.3 mm long; anterior groove occasionally present but usually indiscernible. Ligament area not preserved.

Surface (not including the surfaces of the prodissoconch and the posterior auricle) divisible into three contiguous radial sectors (triangular fields):

(1) Anterior sector with irregular commarginal growth lines, its ventral margin subtending an angle of about 25–35° with the dorsal margin;

(2) Central sector bounded by the anterior sector and the posterior groove, enclosing an angle of about 100–110°, bearing regular, fine, sharply rounded commarginal lirae; lirae somewhat weakening anteroventrally, occasionally obscure on the whole sector; spacing of the lirae narrow during earlier ontogenetic stages and gradually widening with progressing ontogeny;

(3) Posterior sector ventrally bordered by a broad, shallow radial groove that diverges from the dorsal margin at an angle of 35–45° in early ontogenetic stages and 20–25° in late ontogenetic stages; exhibiting broad, closely spaced commarginal undulations; each undulation usually branching into two or three lirae ventrally.

Juvenile shells (10–15 mm long, 6–12 mm high; Figs. 4J, 5): shape variable, ranging from reversed-subtrigonal to subelliptical, generally suboval, occasionally subcircular (Fig. 5D). Posterior sector relatively wide, its ventral margin subtending an angle of about 35–45° with the dorsal margin. Differentiation of the sculptural features of the three sectors not distinct; posterior sector usually without ventrally branching commarginal undulations but exhibiting commarginal lirae that are slightly broader than those on the central sector.

Discussion.—In most specimens of *Enteropleura walleri* sp. nov., the shell sculpture of the central sector consists of fairly distinct, regular commarginal lirae (Figs. 4A, B, D–F, J, M, 5A, B, D). But in some specimens, the commarginal lirae are very weak or even nearly indiscernible (Fig. 4G, H, L). These differing sculptural features might lead to an assignment to different species. However, these variably sculptured shells usually co-occur (e.g., Fig. 4H) and some intermediate forms (Figs. 4C, I, 5C) indicate that the differing sculptural features are due to intraspecific variation. Although these differently sculptured specimens may be found very close to each other on the same slab (e.g., Fig. 4H), the varying sculpture also may partly be due to preservational reasons since these very thin shells certainly were susceptible even to slight differences in taphonomical and diagenetical conditions.

With regard to shell outline, shell size, commarginal sculpture, and presence of a posterior auricle, *Enteropleura walleri* is closely related to the three other species of the *Enteropleura bittneri* group, namely *E. bittneri* Kittl, 1912, *E. jenksi* Hopkin and McRoberts, 2005, and *E. lamellosa* (Kittl, 1912). However, these latter species all have distinct radial shell sculpture which is lacking in *E. walleri*.

Occurrence.—Unit D, Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic); Fengshan District, Guangxi, southwestern China.

Enteropleura guembeli (Mojsisovics, 1874)

Fig. 6.

1874 *Daonella Gümbeli* sp. nov.; Mojsisovics 1874: 8, pl. 3: 12, 13.
1912 *Enteropleura Gümbeli* (Mojsisovics); Kittl 1912: 162, pl. 1: 16, 17.
1974 *Enteropleura guembeli* (Mojsisovics); Chen et al. 1974: 334, pl. 175: 22 [same specimen described by Gu et al. (1976: 225, pl. 38: 18) and Gan and Yin (1978: 351, pl. 118: 6)].
1980 *Enteropleura guembeli* Mojsisovics; Chen 1980: 1192.

Material.—Only the figured right valve, NIGP 15959, from the lower part of the Xinyuan Formation (late Middle Anisian, early Middle Triassic); Bomo area, Xinyuan, Ziyun District, southwestern Guizhou, southwestern China. Although the

specimen was registered with a NIGP repository catalogue number, it apparently has not been handed over to the collections of NIGP and was not available for this study; most probably it is lost. The figure provided herein is a reproduction of that in Chen et al. (1974).

Original description.—Chen et al. (1974: 334, translated from Chinese): "Shell small, subcircular. Hinge line straight and short, about 2/3 of the shell length. Umbo situated slightly anterior to mid-length. Posterior slope of umbo with a shallow groove. Shell surface with 5–6 commarginal lines and fine, weak, closely spaced radial lines."

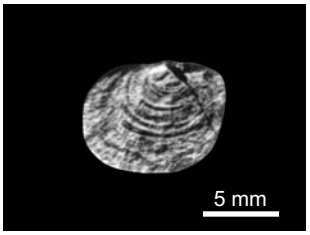


Fig. 6. Halobiid bivalve *Enteropleura guembeli* (Mojsisovics, 1874) from the lower part of the Xinyuan Formation (late Middle Anisian, Middle Triassic), Mobo, Xinyuan, Ziyun District, southwestern Guizhou, southwestern China. Right valve, NIGP 15959; reproduction of Chen et al. (1974: pl. 175: 22).

Re-description.—Shell small, 9 mm long, rounded-subquadrate with the dorsal part being slightly longer than the ventral part; longer than high, height/length ratio about 0.8. Beak orthogyrous, slightly projecting above the dorsal margin, positioned at 0.45 of the shell length from anterior. Dorsal margins slightly descending from the beak, ventral and posterior margins broadly curved; anterior margin curved, but anterior part probably slightly incomplete. Hinge line straight and short, equalling about 0.6 of the shell length; ligament area not preserved; auricles absent. Prodissoconch small, about 1 mm in length. External surface of dissoconch with commarginal sculpture of 5–6 irregular rugae and several very fine lines; rugae restricted to early and middle ontogenetic stages; radial striae very fine and weak, threadlike, limited to the central and posterior sectors.

Discussion.—*Enteropleura guembeli* is a small species with nearly subcircular (slightly longer than high) shell. Its surface exhibits several irregular commarginal rugae and weakly developed radial ribs, and lacks regular and fine commarginal lirae (Mojsisovics 1874: 8, pl. 3: 12, 13; Kittl 1912: 162, pl. 1: 16, 17). These sculptural features distinctly differ from those of the taxa of the *Enteropleura bittneri* group (i.e., *E. bittneri*, *E. jenksi*, *E. lamellosa*, *E. walleri*).

In the original description of the Guizhou specimen, Chen et al. (1974: 334) mentioned a short "shallow groove" on the umbonal part (Fig. 6). However, position and direction of this "groove" seem to differ from those of the grooves generally found in the species of *Enteropleura*, including *E. guembeli*, which indicate the internal ridges. This "groove" may be an artefact. However, the other features of this specimen such as shell shape, shell size, beak, hinge line, and surface sculpture are close to those of the type specimens of *E. guembeli* (Mojsisovics 1874; Kittl 1912). Therefore, the assignment by Chen et al. (1974) is acceptable (e.g., Gu et al. 1976: 225; Gan and Yin 1978: 351; Chen 1980: 1192; Yin 1985: 588; Chen 2004: 659). According to Gan (1983), the Guizhou specimen of *E. guembeli* comes from a dark-green sandy shale of the lower part of the Xinyuan Formation, which yields the ammonoids "*Paraceratites*" cf. *binodosus*, *Judicarites* sp., and *Balatonites* sp., indicating a late Middle Anisian age.

Conclusions

- *Enteropleura walleri* sp. nov. from late Middle Anisian deposits of the central basin facies of the Nanpanjiang Basin in Fengshan District, northwestern Guangxi, southwestern China, widens the knowledge about the genus *Enteropleura*. The new species is characterised by an external sculpture of regular, fine commarginal lirae and a large prodissoconch; it differs from all other congeneric species in the lack of radial sculpture.
- The taxonomic status of *Enteropleura guembeli* reported by Chen et al. (1974) from late Middle Anisian strata of Guizhou, southwestern China, is confirmed and thus the occurrence of small-sized representatives of *Enteropleura* in the basin slope facies of the Nanpanjiang Basin.
- The genus *Enteropleura* comprises five species that may be morphologically subdivided into two species groups, *E. guembeli* group (*E. guembeli* only) and *E. bittneri* group (*E. bittneri*, *E. jenksi*, *E. lamellosa*, *E. walleri*). This subdivision may be of significance for the reconstruction of the phylogenetical relationships of these species.
- The genus *Enteropleura* is morphologically intermediate between *Bositra* and *Daonella*. Its occurrence is restricted to a narrow stratigraphical interval of late Middle Anisian age. Different species of *Enteropleura* have been described from Hungary, Austria, Croatia, Nevada, and southwestern China. Therefore the genus is considered to be of importance with regard to biostratigraphy and the phylogeny of the Halobiidae.

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