

# An early *Daonella* from the Middle Anisian of Guangxi, southwestern China, and its phylogenetical significance

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**Abstract** The late Middle Anisian *Daonella fengshaniensis* sp. nov. from the upper part of the Lower Member of the Banna Formation near Jinya in northwestern Guangxi, southwestern China, represents the earliest appearance of *Daonella* in this region. With regard to stratigraphical occurrence as well as morphological features the new species is in a transitional position between *Enteropleura* and more derived species of *Daonella*. The new species is an early representative of the genus *Daonella* and regarded as phylogenetically being near the genus' origin. It is characterised by a small posterior auricle similar to *Enteropleura* and flat-topped radial ribs resembling later species of *Daonella*. Its anterior shell sector is large. The shell sculpture of juvenile stages closely resembles both *Daonella* and *Enteropleura*, supporting the hypothesis that *Daonella* may have evolved from *Enteropleura*.

**Keywords** Bivalves · *Daonella* · Middle Anisian · China · Taxonomy · Phylogeny

## Introduction

Species of *Enteropleura*, *Daonella*, and *Halobia* of the family Halobiidae are among the most short-lived and

widely distributed flat-shelled bivalves of the Triassic, making them excellent biostratigraphical index fossils in certain facies (e.g. Campbell 1994; McRoberts 1997, 2000, 2010; Schatz 2004, 2005; Waller in Waller and Stanley 2005; Chen and Stiller 2007). Waller (in Waller and Stanley 2005, p. 17, fig. 5) proposed a phylogeny for Triassic "flat clam" genera including *Bositra*, *Enteropleura*, *Daonella*, *Aparimella*, *Halobia*, and others, in which *Daonella* was considered to be derived from *Enteropleura* in the early Middle Triassic and to have evolved into *Aparimella* in the latest Middle Triassic. *Enteropleura* is a short-ranged genus, occurring within a narrow stratigraphical interval of late Middle Anisian age in Nevada, Europe, and southern China (Waller in Waller and Stanley 2005; Chen and Stiller 2007; McRoberts 2010). *Daonella* is younger than *Enteropleura* and generally considered to have its maximum abundance during Late Anisian and Ladinian times (e.g. Kittl 1912; Chen et al. 1992; Campbell 1994; McRoberts 2010). However, recognition of the first appearance of *Daonella* remains controversial (e.g. Campbell 1994).

Mojisovics (1874) regarded the first appearance of *Daonella* to be in the Lower Muschelkalk. According to Schatz (2005, p. 116) the earliest occurrence of *Daonella* in Alpine Europe is in the Late Anisian *Daonella sturi* Zone that is correlated with the upper *Paraceratites trinodosus* Zone. Silberling and Nichols (1982) showed that *Daonella* makes its first appearance in Nevada, USA, during the early Late Anisian, represented by *Daonella americana* SMITH in the lower part of the *Gymnotoceras rotelliformis* Zone. Campbell (1994, p. 34) recognised the first appearance datum (FAD) of *Daonella* in Arctic Svalbard also in the early Late Anisian, represented by *Daonella lindstroemi* MOJSISOVICS. Chen (1982) and Gan (1983) regarded *Daonella guizhouensis* GAN to be the earliest *Daonella* in southern Guizhou, southwestern China. In the Guizhou

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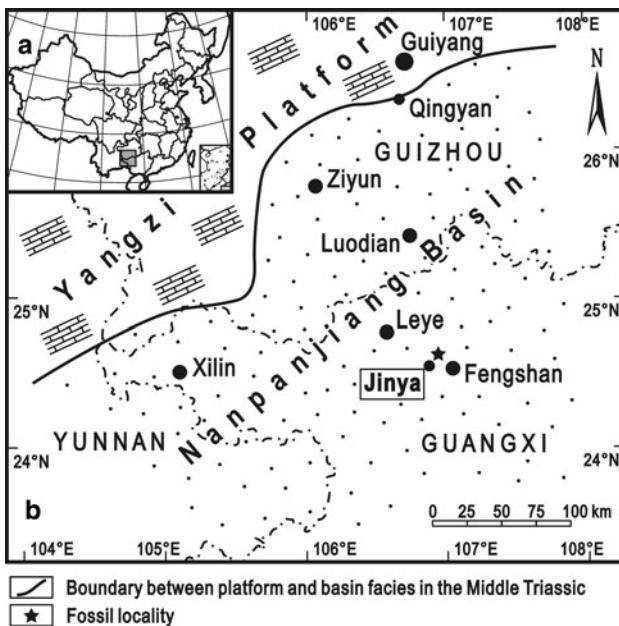
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succession, *D. guizhouensis* occurs in a stratigraphical position about 20–30 m below *D. americana* (Gan 1983); therefore, it is slightly older than the latter species, but most probably also of early Late Anisian age.

On the other hand, based on Begg (1981), Campbell (1994, p. 25) mentioned that the FAD of *Daonella* in New Zealand lies within the Middle Anisian, thus being earlier than the *Daonella* FAD in Nevada, Alpine Europe, Svalbard, and Guizhou. Unfortunately, the study of Begg (1981) is unpublished and was not available for reference. Therefore, it is difficult to correlate the Middle Anisian *Daonella* of New Zealand with the Chinese specimens.

In this contribution we report a new species, *Daonella fengshanensis* sp. nov., from the Jinya section in Fengshan County, northwestern Guangxi, southwestern China (Fig. 1), providing new information on the early evolution of the genus *Daonella*. Although the available specimens of *D. fengshanensis* are relatively poorly preserved, they are of phylogenetical significance and represent the earliest appearance of *Daonella* in southern China (Figs. 2, 3). In the Jinya section, the late Middle Anisian *D. fengshanensis* occurs in a transitional position between *Enteropleura* and more derived species of *Daonella*, about 90–100 m below the *Daonella americana*–*Daonella guizhouensis* beds, and about 9–11 m above the *Enteropleura* bed. Significantly, the morphological features of the new taxon



**Fig. 1** Location of the fossil site near Jinya in Fengshan County, 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) sedimentary facies, indicated by standard symbols (palaeogeographical reconstruction after Chen and Komatsu 2002).

| Age      | NW Guangxi<br>(after Chen et al. 1992, Chen and Stiller 2007) |          |           | SW Guizhou<br>(Gan 1983) |  |
|----------|---|----------|-----------|--------------------------|--|
|          | Xilin - Leye  |          | Fengshan  |                          |  |
| Ladinian | Mb 3  | Lanmu Fm | Third Mb  | Bianyang Formation       |  |
| Late     | Hekou Fm  |          | Second Mb |                          |  |
| Early    | Mb 1  |          | First Mb  |                          |  |
| Anisian  | Mb 4  | Banna Fm | Upper Mb  | Xinyuan Formation        |  |
| Middle   | Mb 3  |          | Lower Mb  |                          |  |
| Early    | Mb 2  |          | E         |                          |  |
| Middle   | Mb 1  |          | D         |                          |  |
| Early    |   |          | C         |                          |  |
| Middle   |   |          | B         |                          |  |
| Early    |   |          | A         |                          |  |

**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)

are intermediate between *Enteropleura* and more derived species of *Daonella*.

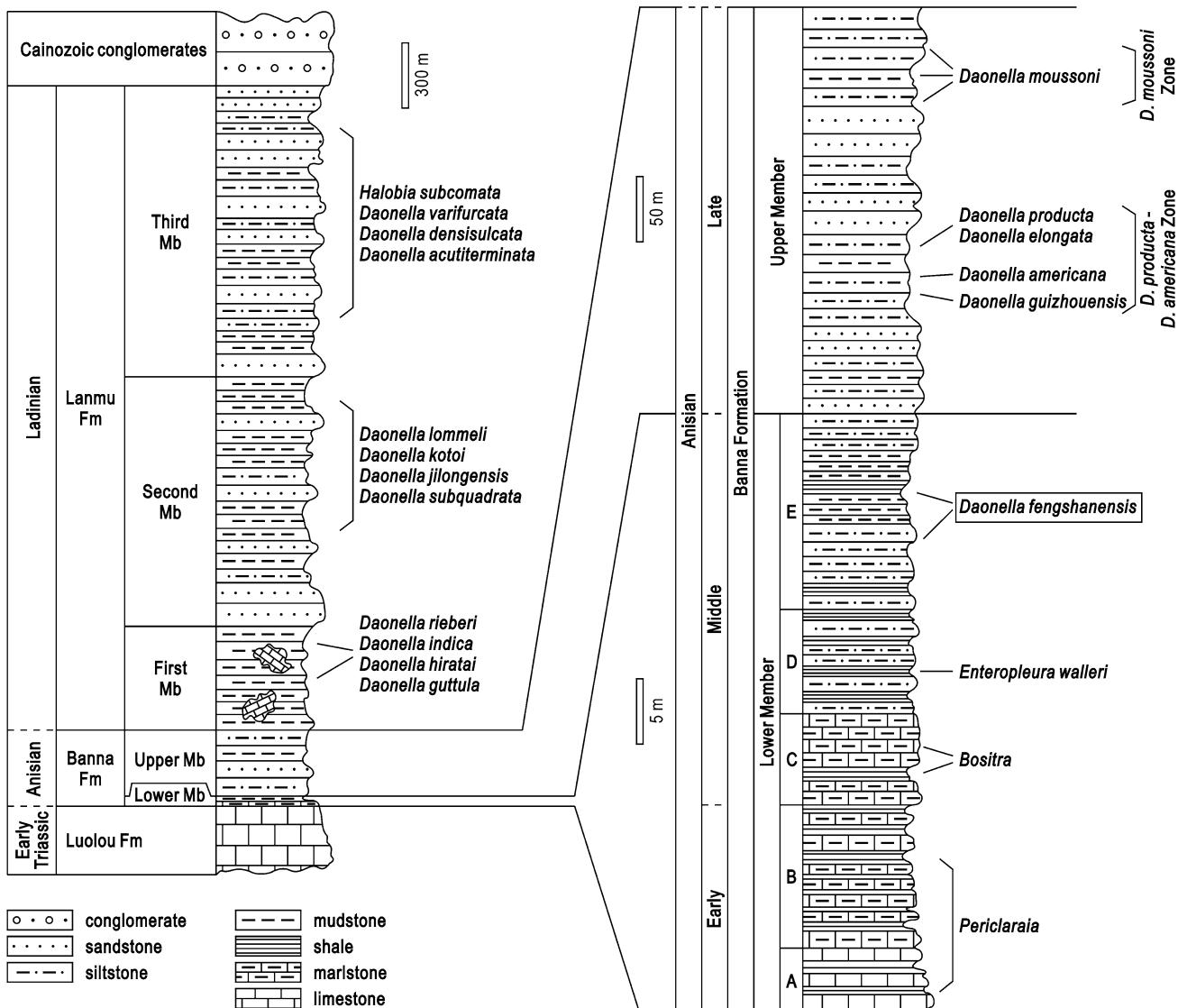
All specimens described in this paper are housed in the collections of the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, in Nanjing, P.R. China.

### Stratigraphical setting

The Middle Triassic in the Fengshan area comprises the Banna Formation (Anisian) and the Lanmu Formation (Ladinian) (Figs. 2, 3). The Banna Formation is subdivided into two members, and the Lanmu Formation into three members (Geological Bureau of Guangxi Zhuang Autonomous Region 1985; Chen et al. 1992). The Lower Member of the Banna Formation consists of finely laminated mudstones, siltstones, and limestones, is about 45–60 m thick, and ranges from Early to Middle Anisian in age. These strata are considered to have been deposited in the central area of the Nanpanjiang Basin (Chen et al. 1992; Chen and Komatsu 2002). Chen and Stiller (2007) further divided the Lower Member of the Banna Formation into five stratigraphical units (Unit A to Unit E in ascending order).

Units A and B consist of limestones and marlstones with intercalations of black calcareous mudstones, in total 15.8 m thick, and yield ammonoids, conodonts, and bivalves. The conodonts and ammonoids indicate an Early Anisian age of these units (Chen and Komatsu 2002; Chen and Stiller 2007).

Unit C is composed of grey marlstones and mudstones, 7 m thick, and yields bivalves of the genus *Bositra* and



**Fig. 3** Stratigraphical and lithological columns of the Middle Triassic in the Fengshan area, northwestern Guangxi, and occurrences of bivalves, with emphasis on the Anisian Banna Formation (*Fm*)

Formation, *Mb* Member; note the different scales for Lower Member and Upper Member of the Banna Formation); taxonomic identifications of the Late Anisian and Ladinian bivalves by Chen et al. (1992)

ammonoids. It may be correlated with the early Middle Anisian *Acrochordiceras hyatti* Zone of Nevada (Chen and Stiller 2007).

Unit D consists of grey siltstones and mudstones, is 8 m thick, and yields the ammonoids *Balatonites cf. balatonicus* and *Gymnites* sp. and the bivalve *Enteropleura walleri*. It is of late Middle Anisian age (Chen and Stiller 2007) and may be correlated with the *Balatonites balatonicus* Zone of Alpine Europe and the *Balatonites shoshonensis* Zone of Nevada (Bucher 1992; Waller and Stanley 2005).

Unit E is made up of brown and grey mudstones and siltstones, 15 m thick, and yields the ammonoids *Balatonites* sp. and *Gymnites* sp. The bivalve *Daonella fengshanensis* sp. nov. occurs in the middle part of this unit, about 9–11 m above the *Enteropleura walleri* bed of Unit

D. The ammonoid specimen from this unit assigned to *Balatonites* sp. is poorly preserved, but its general features are very close to those of *Balatonites cf. balatonicus* from Unit D. Therefore, the age of Unit E is considered to be late Middle Anisian as well (Chen and Stiller 2007).

The Upper Member of the Banna Formation consists of sandstones, siltstones, and mudstones, is in the Fengshan area about 300 m thick, and of Late Anisian age. During Late Anisian times, the region of today's Fengshan area was located in the basin slope area of the Nanpanjiang Basin (Chen et al. 1992; Chen and Komatsu 2002; Chen and Stiller 2007). Chen et al. (1992) recognised two *Daonella* zones in this member, the *Daonella producta*–*Daonella americana* Zone in its lower part, and the *Daonella moussonii* Zone in its upper part. The latter may be correlated

with the *Daonella moussonii*–*Daonella dubia* beds of the latest Anisian *Frechites occidentalis* Zone of Nevada (Silberling and Nichols 1982). The *D. producta*–*D. americana* Zone spans the earlier parts of the Late Anisian. Chen et al. (1992, pp. 407–408) suggested that this zone may be subdivided into two beds: The *Daonella americana* bed in the lower part may be correlated with the *D. americana* beds of the middle Late Anisian *Gymnotoceras rotelliformis* Zone of Nevada (Silberling and Nichols 1982), and the *Daonella producta*–*Daonella elongata* bed in the upper part may be correlated with the *D. elongata* beds of the late Late Anisian *Parafrechites meeki* Zone of Nevada. In the Jinya section of Guangxi, *Daonella guizhouensis*, previously assigned to “*Daonella elongata*” by Chen et al. (1992), occurs about 10 m below the *D. americana* bed.

## Systematic palaeontology

|             |  |
|-------------|--|
| Class       | Bivalvia LINNAEUS 1758   |
| Subclass    | Autolamellibranchiata GROBBEN 1894                                   |
| Superorder  | Pteriomorphia BEURLEN 1944 (emend. Waller 1978)                      |
| Order       | Pterioida NEWELL 1965 (emend. Waller 1978)                           |
| Suborder    | Pterioidina NEWELL 1965 (emend. Waller 1978)                         |
| Superfamily | Posidonioidea FRECH 1909 (emend. Waller, in Waller and Stanley 2005) |
| Family      | Halobiidae KITTL 1912 (emend. Waller, in Waller and Stanley 2005)    |

### Genus *Daonella* MOJSISOVICS 1874

Type species—*Halobia lommeli* WISSMANN 1841; subsequent designation by Diener 1923, p. 46.

Remarks—Taxonomy and systematics of the Middle Triassic “flat clam” genera *Bositra* DE GREGORIO 1886, *Enteropleura* KITTL 1912, and *Daonella* MOJSISOVICS 1874 have been discussed by various authors (e.g. Kittl 1912; Campbell 1994; Waller in Waller and Stanley 2005) and remain controversial. Due to preservation reasons, internal features such as ligament, resilifer, and muscle scars are unknown in most species of these genera, making reliable assignments sometimes difficult. In general, ligament features are particularly important for bivalve taxonomy, but in some of the taxa discussed here they are less significant for genus-level assignment; for example, the alivincular ligament of *Enteropleura* is very similar to that of *Bositra*, and the lamellar ligament of *Daonella* resembles that of *Apirimella* CAMPBELL 1994 and *Halobia* BRONN 1830 (Waller in Waller and Stanley 2005, pp. 17–18). Although the external shell sculpture may vary ontogenetically and is susceptible to preservation issues, external shell features nevertheless may provide clues for taxonomy and systematics in the case

of well-documented taxa. Waller (in Waller and Stanley 2005) and Hopkin and McRoberts (2005, p. 797) also regarded the external shell sculpture as an important trait for distinguishing the genera *Bositra*, *Enteropleura*, and *Daonella*. The new taxon described herein and regarded as a very early representative of the genus *Daonella* shows external shell features intermediate between *Enteropleura* and *Daonella*, and its internal shell features are unknown.

*Bositra* is characterised by regular commarginal ribs; radial shell sculpture is lacking, or the radial riblets are fine and weak, weaker than the commarginal sculpture. Anterior and posterior auricles may be present or absent. Following Waller (in Waller and Stanley 2005) and not adopting the view of McRoberts (2010), *Peribositria* KURUSHIN & TRUSHCHELEV 1989 is regarded as a junior synonym of *Bositra*. Waterhouse (2008) erected the family *Bositridae* for Triassic and Jurassic *Bositra*-like bivalves. Here, *Bositridae* WATERHOUSE 2008 is regarded as a junior synonym of *Posidoniidae* FRECH 1909, and *Bositra* is considered to be a posidoniid.

*Enteropleura* shows commarginal ribbing and in most species radial threads or ribs; the commarginal sculpture is stronger than the radial sculpture; *Enteropleura walleri* CHEN & STILLER 2007 lacks radial sculpture. The radial ribs, if present, are fine and rounded (Mojsisovics 1874; Kittl 1912; Waller in Waller and Stanley 2005; Hopkin and McRoberts 2005). No anterior auricle is developed. A narrow and small posterior auricle is present in some species, in other species the posterior auricle has not (yet) been observed (maybe due to insufficient preservation or documentation). Here, *Enteropleura* and *Daonella* are placed in the family *Halobiidae* (order Pterioida).

Waterhouse (2008) erected the genus *Wallerobia* for species of *Enteropleura* with radial shell sculpture and small posterior auricles, and placed the new genus in his new family *Bositridae*. *Enteropleura* sensu Waterhouse (2008) lacks anterior and posterior auricles as well as radial shell sculpture. Herein, the genus *Wallerobia* WATERHOUSE 2008 is rejected and regarded as a junior synonym of *Enteropleura*, because the morphological features emphasised by Waterhouse (2008) to distinguish *Wallerobia* from *Enteropleura* are only of species-level significance, and the character of the morphological differences does not justify the formal erection of a new genus-level taxon (also see discussion on species-groups in *Enteropleura* in Chen and Stiller 2007, p. 58). The always very small posterior auricle in *Enteropleura* varies in size in different species (Waller in Waller and Stanley 2005; Hopkin and McRoberts 2005; Chen and Stiller 2007) and is, due to its tiny and fragile character, not easily preserved. Some species of *Enteropleura* are not well documented, and therefore it remains unclear whether they had a tiny posterior auricle or not, because the auricle may have been overlooked or not been

preserved. The somewhat varying external shell sculpture with variably distinct radial riblets is only of species-level significance. For example, *Enteropleura walleri* has a small posterior auricle but lacks radial shell sculpture (Chen and Stiller 2007). Waterhouse (2008, p. 178) described this species as being characterised by “close-set commarginal wrinkles and very faint radial ribs”, but he had not seen the specimens. His “very faint radial ribs” are preservation artefacts, *E. walleri* lacks radial shell sculpture. If following the genus-level classification of Waterhouse (2008), *E. walleri* with its mosaic of morphological features characteristic for *Enteropleura* and “*Wallerobia*”, would be difficult to assign on the genus-level.

*Daonella* is characterised by commarginal and radial ribbing with the radial sculpture being (much) stronger than the commarginal sculpture in adult ontogenetical stages; the radial ribs in general are relatively strong, broad, and flat-topped. *Daonella* lacks auricles. However, there are few exceptions in early representatives of this genus: *Daonella boeckhi* Mojsisovics 1874 shows commarginal shell sculpture and only weak radial sculpture; it lacks auricles. *Daonella fengshanensis* described herein has a narrow and small posterior auricle but exhibits typical *Daonella*-type shell sculpture.

*Daonella fengshanensis* sp. nov. (Figs. 4, 5, 6, 7)

1992 *Daonella* spp.—Chen et al.: p. 405.

2002 *Daonella dianana* Guo—Chen and Komatsu: p. 436, p. 442.

2007 *Daonella* sp.—Chen and Stiller: p. 55, p. 56.

**Etymology**—Named after Fengshan County in which the type locality is located.

**Types**—Holotype, NIGP 148212 (Fig. 4h–i); paratypes, NIGP 148209 (Fig. 4a–b), NIGP 148211 (Fig. 4f–g), NIGP 148213 (Fig. 4c), NIGP 148214-2 (Fig. 5a). All type specimens from Unit E of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic), Jinya, Fengshan County, northwestern Guangxi, southwestern China.

**Other material examined**—More than 55 external and internal moulds of left and right valves, and numerous fragments, from the same strata and locality as the type specimens (NIGP 148209–148225).

**Measurements**—Holotype (NIGP 148212) length about 43 mm, height >20 mm (specimen ventrally incomplete).

**Occurrence**—Hitherto only known from Unit E of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic), Jinya, Fengshan County, northwestern Guangxi, southwestern China.

**Diagnosis**—*Daonella* with a small and narrow posterior auricle; anterior sector large and smooth, central sector with flat-topped radial ribs; pre-adult growth stages with both rounded and flat-topped radial ribs.

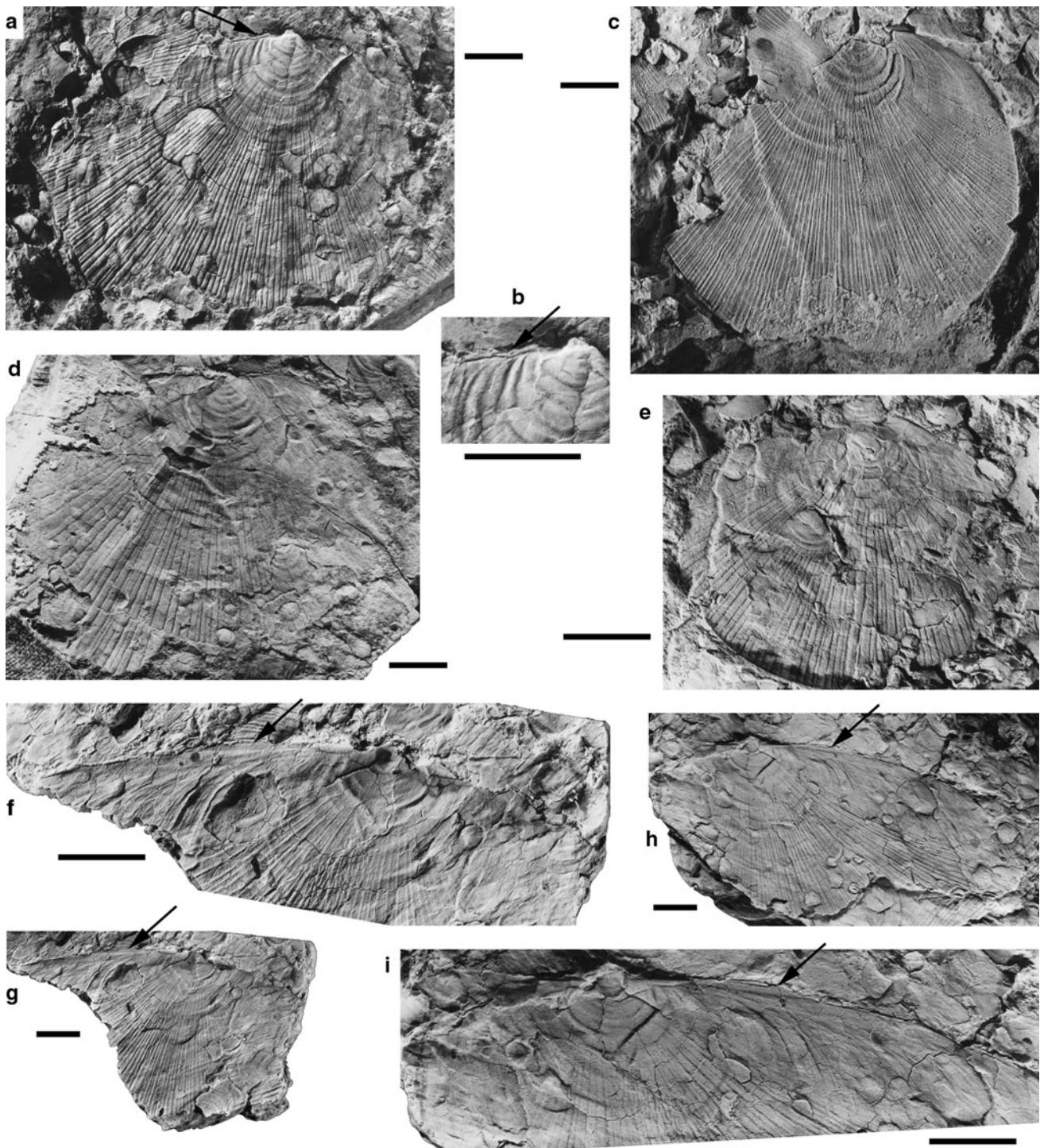
**Description**—Shell outline subcircular to ovate; size small to medium, with length generally 20–30 mm, but up to about 40 mm; shell longer than high with height/length ratio about 0.8–0.9, of low convexity. Beaks small, orthogyrous, located anterior to mid-length, slightly protruding above the dorsal margin. Dorsal margins gently convex or sometimes nearly straight. Hinge line long, length equalling about two-third of the shell length or more, commonly asymmetrical, with posterior hinge line longer than anterior hinge line. Anterior auricle absent. Posterior auricle small and narrow, weakly inflated, separated from disk by narrow sulcus; dorsal and posterior margin of auricle forming obtuse angle of about 145°–165°, angle subtended by dorsal margin and base of auricle about 5°–10°; surface of auricle smooth (Figs. 4f–i, 5a). Ligament and muscle scars unknown due to preservational reasons. Prodissococonch subcircular, smooth, moderately sized, length about 0.5–0.8 mm.

**Description: Surface of shell**—(Not including smooth surfaces of prodissococonch and small posterior auricle.) Shell surface divisible into three sectors (triangular fields): (1) anterior sector, distinguished only by lack of radial shell sculpture, its ventral margin subtending an angle of about 60°–80° with the dorsal margin; (2) central sector, sculptured by radial ribs and commarginal undulations (pre-adult stages) or lirae (adult stages), sector margins forming an angle of about 90°–100°; and (3) posterior sector, slightly inflated, sculptured by commarginal undulations/lirae only or sometimes additionally by very weak radial furrows, its ventral margin subtending an angle of about 20°–30° with the dorsal margin.

**Description: Shell sculpture**—Broad commarginal rugae or undulations present in early ontogeny, variably developed but generally more distinct on the posterior sector than on the anterior and central sectors; adult shell portions only with weak to indistinct commarginal lirae. Radial ribs in pre-adult and adult growth stages restricted to central sector, straight, flat-topped, regularly and densely spaced, generally about equal in strength; radial ribs separated by narrow and shallow furrows of two orders; primary furrows starting at about 3–5 mm from beak; secondary furrows beginning at 4–6 mm from beak.

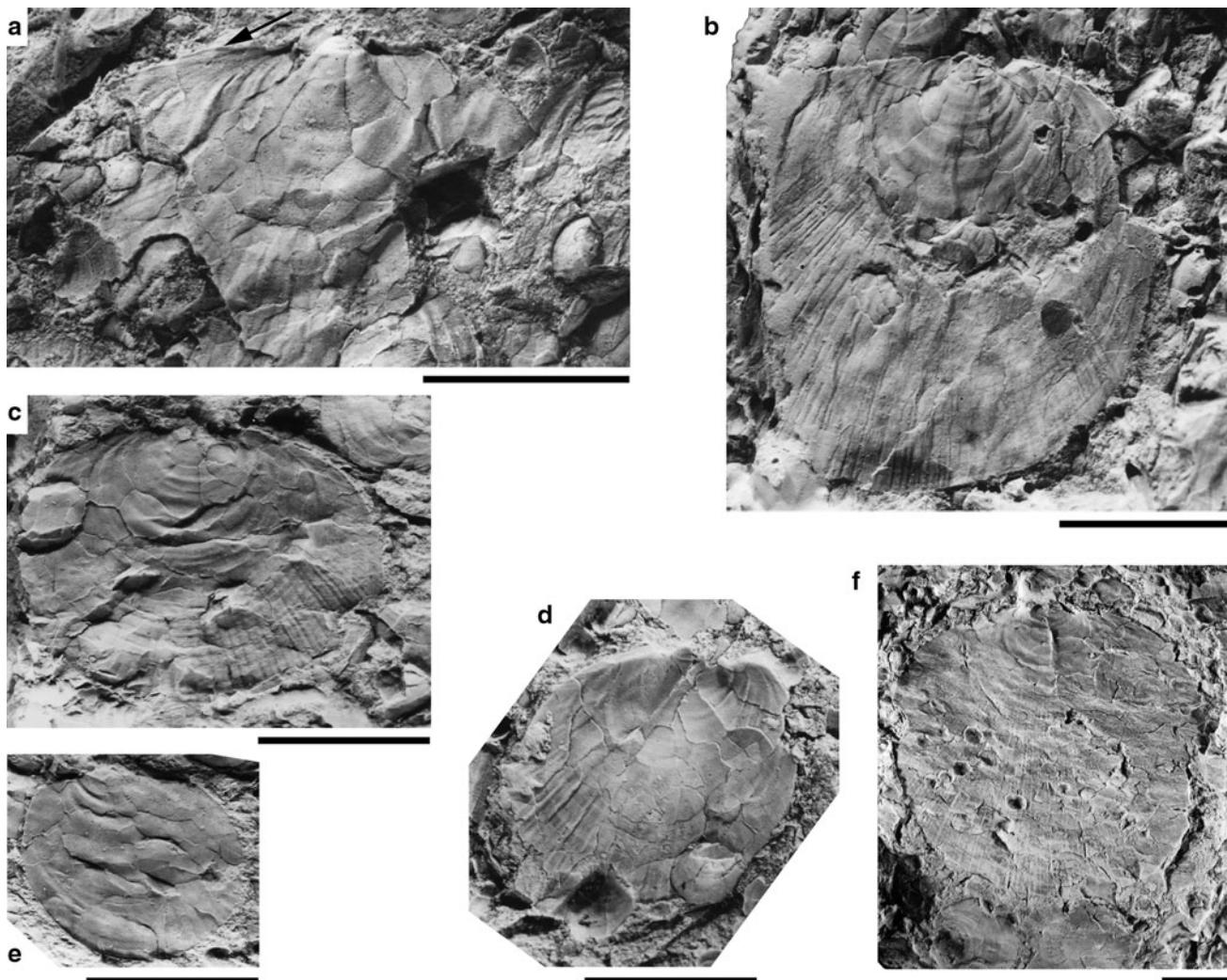
Four pre-adult growth stages distinguishable based on the surface sculpture of specimens with shell lengths of less than 15 mm:

1. Stage A, shell very small, length 3–6 mm (Figs. 6a, c, 7d, f; some specimens in Fig. 7a), sculptured by commarginal undulations or both commarginal undulations and radial riblets; radial riblets, if present, very weak and short, rounded, restricted to the marginal ventral part (Figs. 6c, 7d);



**Fig. 4** *Daonella fengshanensis* sp. nov. All specimens composite moulds, from Unit E of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic), Jinya, Fengshan County, northwestern Guangxi, southwestern China. **a, b** NIGP 148209, paratype, right valve; **b** detail of **a**, showing posterodorsal part of right valve with posterior auricle (deformed and damaged). **c** NIGP

148213, paratype, external mould of left valve. **d** NIGP 148210, right valve. **e** NIGP 148214-1, right valve. **f, g** NIGP 148211, paratype, external mould of left valve; counterpart of NIGP 148212; **f** detail of **g**. **h, i** NIGP 148212, holotype, left valve; counterpart of NIGP 148211; **i** detail of **h**. All scale bars 5 mm; arrows pointing to posterior auricles



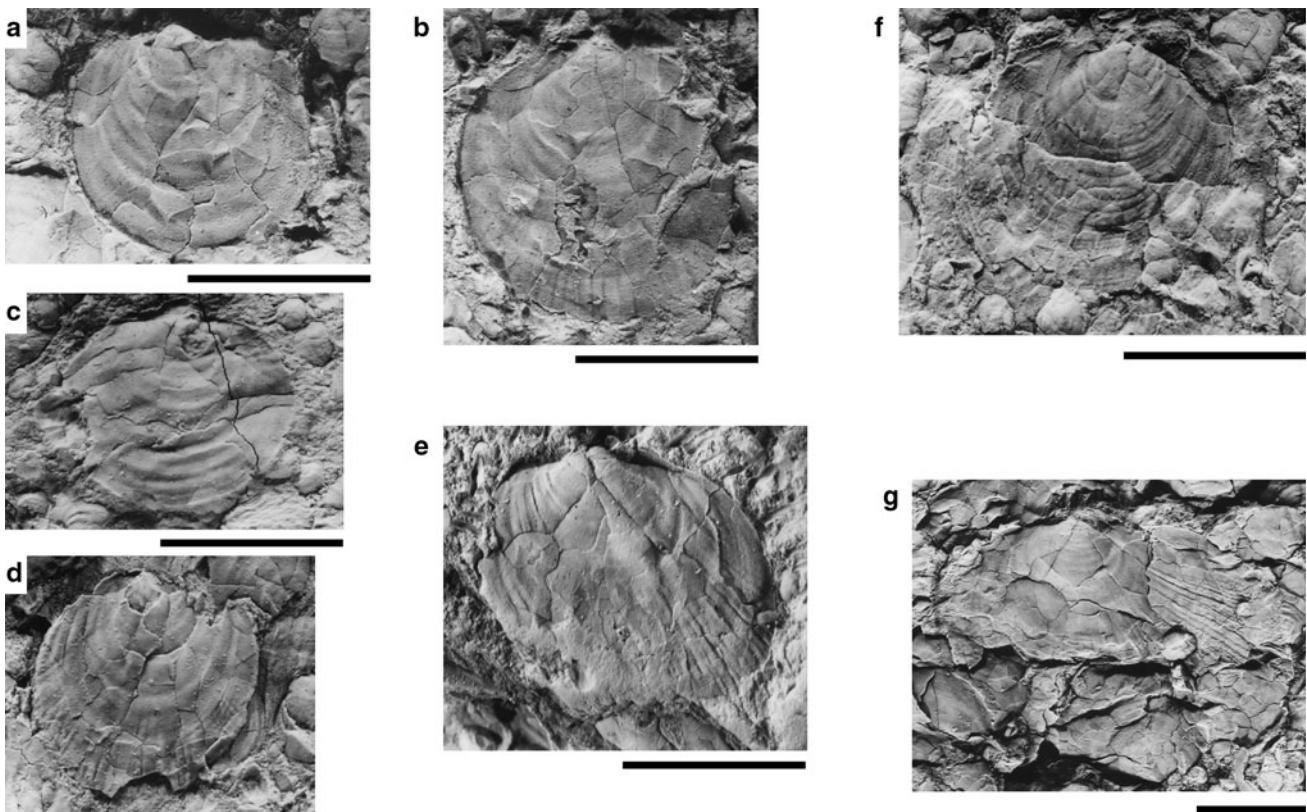
**Fig. 5** *Daonella fengshanensis* sp. nov. All specimens composite moulds, from Unit E of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic), Jinya, Fengshan County, northwestern Guangxi, southwestern China. **a** NIGP148214-2, paratype, dorsal part of right valve, showing the shell sculpture of the pre-adult growth stage D; arrow pointing to posterior auricle. **b** NIGP 148216-1, right valve, showing the shell sculpture of the pre-adult

growth stage D. **c** NIGP 148215, left valve, showing shell sculpture intermediate between the pre-adult growth stages B and C. **d** NIGP 148216-3, external mould of left valve, showing shell sculpture intermediate between the pre-adult growth stages B and C. **e** NIGP 148218, left valve, showing the shell sculpture of the pre-adult growth stage B. **f** NIGP 148216-2, left valve. All scale bars 5 mm

2. Stage B, shell length about 4–9 mm (Figs. 5e, 6b, d–e, 7c, e), sculptured by commarginal undulations and radial riblets; radial riblets very fine, thread-like, densely spaced, rounded, restricted to the ventral quarter to third of the central sector;
3. Stage C, shell length 7–13 mm (Figs. 5c–d, 7b, g); commarginal ribs becoming finer ventrally; both flat-topped radial ribs and rounded radial riblets present, limited to the ventral half of the central sector; flat-topped radial ribs narrowly spaced and separated by shallow furrows, increasing in number by branching; rounded riblets very fine and weak; specimens of Fig. 5c and d showing features intermediate between stages B and C;

4. Stage D, shell length 8–15 mm (Figs. 5a–b, 6f–g); radial flat-topped ribs relatively distinctly developed, covering more than the ventral half of the central sector; rounded riblets disappearing; specimen of Fig. 6f showing features intermediate between stages C and D.

**Remarks**—The shell sculpture of *Daonella fengshanensis* sp. nov., consisting mainly of flat-topped radial ribs, is basically similar to that of later, more derived species of the genus *Daonella* (e.g. Mojsisovics 1874; Kittl 1912; Campbell 1994; McRoberts 2000). The new species is characterised by the presence of a posterior auricle (Figs. 4a–b, f–i, 5a), in contrast to all later species of



**Fig. 6** *Daonella fengshanensis* sp. nov. All specimens composite moulds, from Unit E of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic), Jinya, Fengshan County, northwestern Guangxi, southwestern China. **a** NIGP 148222-1, left valve, showing the shell sculpture of the pre-adult growth stage A. **b** NIGP 148222-2, left valve, showing the shell sculpture of the pre-adult growth stage B. **c** NIGP 148223-2, right valve, showing the shell

sculpture of the pre-adult growth stage A. **d** NIGP 148223-3, right valve, showing the shell sculpture of the pre-adult growth stage B. **e** NIGP 148220-1, left valve, showing the shell sculpture of the pre-adult growth stage B. **f** NIGP 148225, right valve, showing shell sculpture intermediate between the pre-adult growth stages C and D. **g** NIGP 148221-1, left valve, showing the shell sculpture of the pre-adult growth stage D. All scale bars 5 mm

*Daonella* that lack auricles (e.g. Campbell 1994; Waller in Waller and Stanley 2005). The posterior auricle of *D. fengshanensis* is very similar to the posterior auricles in some species of *Enteropleura* (Waller in Waller and Stanley 2005; Hopkin and McRoberts 2005; Chen and Stiller 2007). This indicates that *D. fengshanensis* is closely related not only to *Daonella* but also to *Enteropleura*.

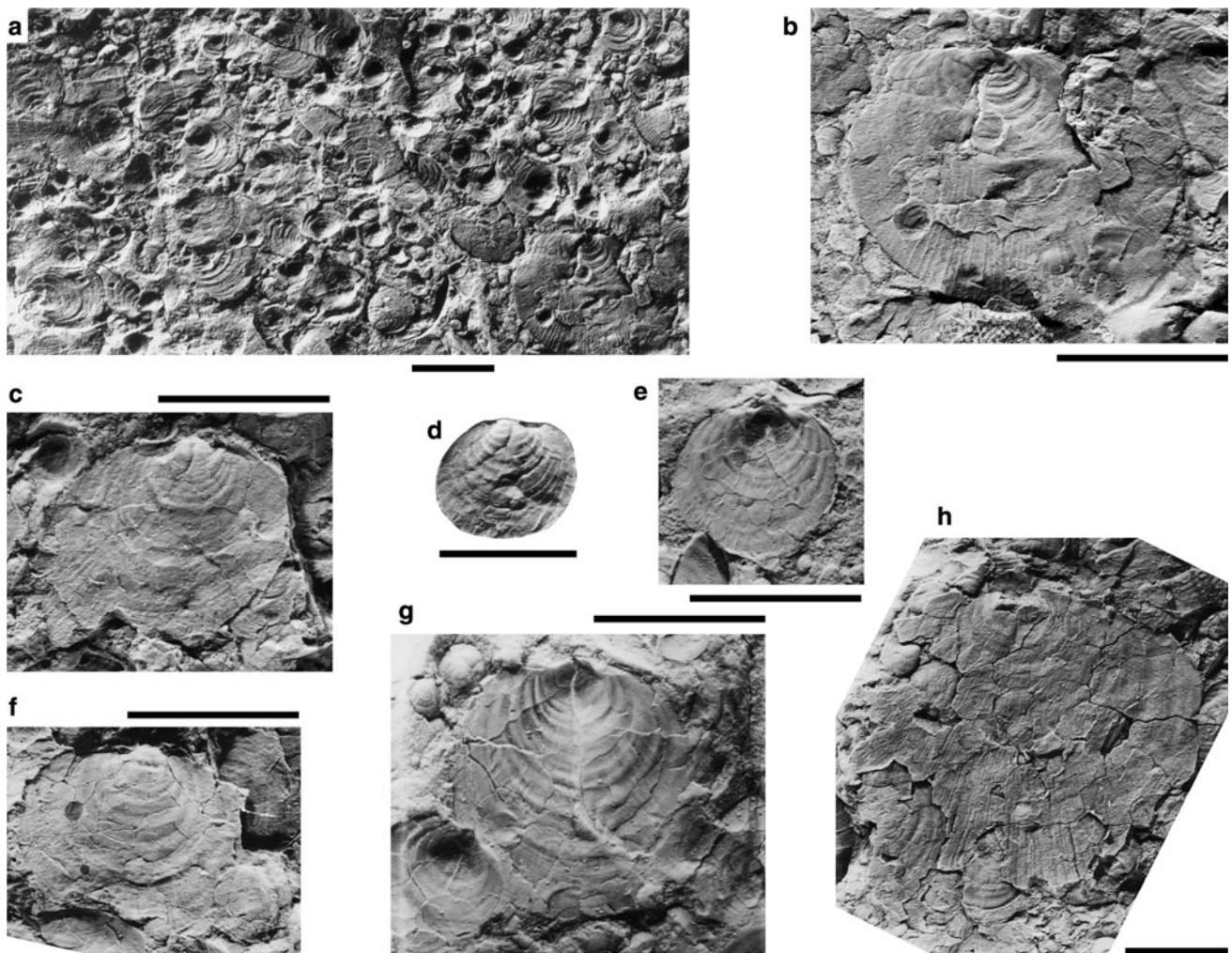
*Daonella boeckhi* also is an early representative of the genus *Daonella* and shows some morphological features different from later congeneric species (see above). It differs from *D. fengshanensis* in lacking a posterior auricle and flat-topped radial ribs.

Guo (1985, pl. 15: 11, 12) reported a “primitive” *Daonella*, assigned to *Daonella dianana* Guo 1985, from the Anisian of Funing, Yunnan, southwestern China. The shell sculpture of the anterior and central sectors of *D. dianana* is similar to that of *D. fengshanensis*. But *D. dianana* has no posterior auricle, and its radial ribs on the central sector are more closely spaced than those in *D. fengshanensis*. Moreover, *D. dianana* probably does not

represent adult growth stages but juvenile stages of a *Daonella*, because the documented shells are fairly small (less than 20 mm long) and their radial ribs are limited to the ventral half of the shell surface.

Concerning shell shape and sculpture, *D. fengshanensis* is closest to *Daonella luganensis* RIEBER 1969 and *Daonella pseudomoussonii* RIEBER 1969 from the latest Anisian of the southern Alps (Rieber 1969, 1973). It differs from the latter two species in the presence of a small and narrow posterior auricle. Furthermore, in *D. fengshanensis* the anterior sector is larger and the radial ribs and furrows on the central sector in early ontogeny are less distinctly developed than in the Alpine species.

*Daonella fengshanensis* is a taxon somewhat intermediate between *Enteropleura* and *Daonella* with regard to its morphological features and its stratigraphical occurrence. If regarding the presence of a small posterior auricle as taxonomically more important than the shell sculpture, *D. fengshanensis* may be assigned to *Enteropleura* as well. However, the species apparently lacks the internal ridges



**Fig. 7** *Daonella fengshanensis* sp. nov. All specimens composite moulds, from Unit E of the Lower Member of the Banna Formation (late Middle Anisian, early Middle Triassic), Jinya, Fengshan County, northwestern Guangxi, southwestern China. **a** NIGP 148224, valves of juvenile individuals, external and internal moulds. **b** NIGP 148224-5, external mould of right valve, showing the shell sculpture of the pre-adult growth stage C. **c** NIGP 148224-2, right valve, showing the shell sculpture of the pre-adult growth stage B. **d** NIGP 148224-7,

right valve, showing the shell sculpture of the pre-adult growth stage A; note the short radial riblets on the ventral part of the central sector. **e** NIGP 148224-4, external mould of left valve, showing the shell sculpture of the pre-adult growth stage B. **f** NIGP 148224-3, right valve, showing the shell sculpture of the pre-adult growth stage A. **g** NIGP 148224-6, external mould of left valve, showing the shell sculpture of the pre-adult growth stage C. **h** NIGP 148224-1, (?) right valve. All scale bars 5 mm

typical for *Enteropleura*, and its external shell sculpture is not of the *Enteropleura* type but of the *Daonella* type. Following Waller (in Waller and Stanley 2005) and Hopkin and McRoberts (2005) and regarding the external shell sculpture as an important trait, the new species is assigned to *Daonella*. The small posterior auricle most probably represents a character retained from the ancestors in the evolutionary lineage from *Bositra* via *Enteropleura* to *Daonella*. It is regarded to represent a species-level character.

The pre-adult ontogeny of *D. fengshanensis* also indicates that this species is closely related to more derived species of *Daonella* and at the same time phylogenetically

connected to *Enteropleura* and *Bositra*. The shell sculpture of stage A (Figs. 6a, c, 7d, f), characterised by commarginal undulations, sometimes additionally with short radial riblets on the marginal ventral part (Figs. 6c, 7d), resembles that of *Bositra*. The radial sculpture of stage B (Figs. 5e, 6b, d–e, 7c, e), consisting of fine, rounded riblets, is very similar to that of some species of *Enteropleura*, e.g. *Enteropleura guembeli* Mojsisovics 1874 (Mojsisovics 1874; Kittl 1912). The shell sculpture of stage C (Figs. 5c–d, 7b, g), combining *Daonella*-type ribs with *Enteropleura*-type riblets, may indicate phylogenetical linkage between *Enteropleura* and *Daonella*. The shell sculpture of stage D (Figs. 5a–b, 6f–g), consisting only of well developed

*Daonella*-type radial ribs, is already very close to that of the adult stage of the species (Figs. 4a–i, 5f, 7h). These features indicate that *D. fengshanensis* is an early representative of the genus *Daonella*, phylogenetically situated near the origin of this genus. *Daonella* may have evolved from a species of *Enteropleura*, and this lineage may be ultimately rooted in *Bositra*, thus suggesting an evolutionary lineage from *Bositra* via *Enteropleura* to *Daonella*.

Some authors referred to a dorsal shell portion in *Halobia* as a “posterior auricle” (e.g. Campbell 1994, p. 38, fig. 3.1; McRoberts 2000, p. 600, fig. 2). However, this shell part is not homologous with the posterior auricles of *Daonella fengshanensis* and *Enteropleura*, and also not homologous with the posterior auricles of alate pterioids and pectinoids. It rather is merely a part of the shell disk (Waller in Waller and Stanley 2005, p. 18).

## Conclusions

With regard to stratigraphical occurrence as well as external shell morphology the late Middle Anisian *Daonella fengshanensis* sp. nov. from southwestern China is in a transitional position between *Enteropleura* and more derived species of *Daonella*. The new species is an early representative of the genus *Daonella* and regarded as phylogenetically being near the genus’ origin.

The characteristics of the external shell sculpture and those regarding the auricles in combination with the stratigraphical succession (see Fig. 3; for general stratigraphical succession of the genera see Waller in Waller and Stanley 2005 and McRoberts 2010) suggest an evolutionary lineage from *Bositra* via *Enteropleura* to *Daonella*, in which the morphological development may be summarised as (1) gradual strengthening of the radial shell sculpture (2) rounded radial ribs developing into flat-topped radial ribs and (3) gradual reduction or loss of the auricles. In earliest *Daonella* more ancestral features occasionally are retained in single species, e.g. very weak radial sculpture in *D. boeckhi* (resembling *Bositra*) or small posterior auricle in *D. fengshanensis* (resembling *Enteropleura*). This may be interpreted as supporting the hypothesis of this phylogenetical lineage. However, whether these morphological changes really mark an evolutionary lineage needs to be further explored, taking also into consideration internal shell features such as ligament and resilifer characteristics that hitherto are unknown for most of the species concerned.

The sequence of ontogenetical stages observed in *D. fengshanensis* may suggest a peramorphosis in the evolution of radial ribbing characteristics in this assumed lineage. Early ontogenetical stages of *D. fengshanensis* appear to preserve ancestral states with the earliest

ontogenetical stage resembling *Bositra*, followed by stages resembling *Enteropleura*, and finally leading to typically *Daonella*-type radial ribbing in adult stages. Although similar ontogenetical sequences can be found in many other bivalves, and external shell sculpture features generally are somewhat variable and susceptible to preservation issues, this ontogenetical sequence in *D. fengshanensis* may be interpreted as a further clue to the supposed evolutionary lineage, especially when considered in connection with the stratigraphical occurrences of the genera concerned.

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