

First record of *Pojetaia runnegari* Jell, 1980 and *Fordilla* Barrande, 1881 from the Middle East (Taurus Mountains, Turkey) and critical review of Cambrian bivalves

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Abstract Cambrian bivalves from the Middle East are reported here for the first time. They come from early “Middle Cambrian” and latest “Early Cambrian” limestones of the lower Çal Tepe Formation at the type locality (near Seydişehir, western Taurides). The majority of the new findings consists of *Pojetaia runnegari* Jell, 1980, but a few specimens of *Fordilla* sp. represent the first report of this genus from “Middle Cambrian” strata. Based on a compilation of the hitherto reported, but mostly revised Cambrian bivalves, the today widely accepted taxa are discussed. The genera *Pojetaia* Jell, 1980 and *Fordilla* Barrande, 1881 are critically evaluated, and three valid species are included in *Pojetaia*: *P. runnegari* Jell, 1980, *P. sarhroensis* Geyer and Streng, 1998, and—with limitations—*P. ostseensis* Hinz-Schallreuter, 1995. *Fordilla* also includes three species: *F. troyensis* Barrande, 1881, *F. sibirica* Krasilova, 1977, and *F. germanica* Elicki, 1994. The Cambrian genera *Tuarangia* MacKinnon, 1982, *Camya* Hinz-Schallreuter, 1995, and *Arhouria* Geyer and Streng, 1998 most probably belong to the class Bivalvia. Palaeoecologically, the Cambrian bivalves of the Western Perigondwanan shelf seem to occur in a relatively small window of low-energy, subtidal, open-marine, warm-water conditions on a muddy carbonate ramp or platform with reduced sedimentation rate. The frequently interpreted

infaunal mode of life of *Pojetaia* and *Fordilla* is questioned by observations of similarly organized modern bivalves. The palaeogeographical distribution of *Pojetaia* and *Fordilla* is discussed with respect to their early ontogeny and to differences in the recent state of knowledge on shelly fossils from Cambrian carbonate successions of Perigondwana.

Keywords Cambrian · Bivalvia · Pelecypoda · small shelly fossils · Çal Tepe Formation · Turkey

Zusammenfassung Erstmals für den Mittleren Osten werden Funde kambrischer Muscheln gemeldet. Sie entstammen Kalksteinen untermittelkambischer und höchstunterkambrischer Bereiche der tieferen Çal Tepe Formation an der Typuslokalität Çal Tepe (nahe Seydişehir) im westlichen Taurusgebirge. Die Muscheln werden überwiegend durch die Art *Pojetaia runnegari* Jell, 1980 und untergeordnet durch *Fordilla* sp. repräsentiert. Letztere stellt den ersten Nachweis dieser Gattung im „Mittelkambrium“ überhaupt dar. Ausgehend von einer Zusammenstellung der bisher beschriebenen und größtenteils wieder revidierten kambrischen Muscheln, werden die heute weitgehend akzeptierten Formen diskutiert. Insbesondere für die Gattungen *Pojetaia* Jell, 1980 und *Fordilla* Barrande, 1881 und deren Arten werden taxonomisch verwendbare Merkmale kritisch bewertet. Danach ergeben sich im Bestand von *Pojetaia* folgende gültige Arten: *P. runnegari* Jell, 1980, *P. sarhroensis* Geyer and Streng, 1998 und—mit Einschränkung—*P. ostseensis* Hinz-Schallreuter, 1995. In der Gattung *Fordilla* werden die Arten *F. troyensis* Barrande, 1881, *F. sibirica* Krasilova, 1977 und *F. germanica* Elicki, 1994 geführt. Als höchstwahrscheinlich den Bivalvia zuzuordnende, weitere kambrische Gattungen werden *Tuarangia* MacKinnon,

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1982, *Camya* Hinz-Schallreuter, 1995 und *Arhouria* Geyer and Streng, 1998 angesehen. Paläoökologisch scheinen die kambrischen Muscheln des Perigondwanaschelfs innerhalb eines relativ schmalen Fensters aufzutreten, welches niedrigenergetische, subtidale, offenmarine Warmwasserverhältnisse auf einer feinkörnigen Karbonatrampe oder -plattform mit geringer Sedimentationsrate repräsentiert. Die zumeist interpretierte, infaunale Lebensweise von *Pojetaia* und *Fordilla* erscheint im Vergleich mit ähnlich gebauten rezenten Muscheln als nicht hinreichend belegt. Die paläogeographische Verbreitung von *Pojetaia* und *Fordilla* wird mit Blick auf deren frühe Ontogenese und hinsichtlich des Bearbeitungsstandes von Schalenfossilien kambrischer Karbonatfolgen Perigondwanas diskutiert.

Schlüsselwörter Kambrium · Bivalvia · Pelecypoda · *small shelly* Fossilien · Çal Tepe Formation · Türkei

Introduction

Palaeontological data from the Cambrian period of the eastern Mediterranean are restricted to a few regions of the Turkish and the Arabian plates, but mainly work on trilobites and brachiopods has been reported. Non-trilobitic and non-brachiopod Cambrian fossils are sporadically mentioned from Jordan, Israel, and Turkey (overviews in Rushton and Powell 1998; Sarmiento et al. 2001; Shinaq and Elicki 2007). The two last-mentioned references are the only papers on investigations of *small shelly fossils*, although many recent investigations in the western Mediterranean and in Central Europe have shown that Cambrian *small shelly fossils* have a great potential for reconstruction of palaeo-environments and palaeogeography (Elicki 1994, 1998, 2005, 2007; Fernández-Remolar 2001; Elicki and Wotte 2003; Elicki and Pillola 2004; Gubanov et al. 2004; Wotte 2006).

This paper presents the first results of a project on Cambrian *small shelly* faunas from Turkey and is focused on bivalves. The project will contribute to the reconstruction of depositional conditions and of the palaeogeography of the western Gondwana shelf during the Cambrian period and to the clarification of trans-regional relations of the Mediterranean faunas to those farther East.

Although the global chronostratigraphic subdivision of the Cambrian system by the *International Commission on Stratigraphy (ICS)* has been introduced, most workers still use the traditional terms Lower, Middle, and Upper Cambrian. The new stratigraphic subdivision (Babcock and Peng 2007) is still in progress, and not yet all of the Cambrian series and stages have been named and defined by GSSP (for the actual state of affairs, see the ICP website at

<http://www.stratigraphy.org>). The consensus on the subdivision of the Cambrian system is into four series consisting of ten stages. At present, lower boundaries of two series and four stages are defined. Following this new chronostratigraphic subdivision, the traditional “Lower Cambrian/Early Cambrian” approximately corresponds to the two lower series (Terreneuvean and unnamed “series 2”), the traditional “Middle Cambrian” corresponds approximately to unnamed “series 3,” and the traditional “Upper Cambrian/Late Cambrian” corresponds approximately to the Furonian. Because of the still unnamed Cambrian series and stages, and for better reading, in this paper we use “Early Cambrian”, “Middle Cambrian”, and “Late Cambrian” (written in quotation marks) as informal terms.

The figured specimens are housed in the Geological Institute of Freiberg University under collection number FG 600.

Geological setting

The Taurus Mountains represent the western segment of the Taurides, located in the southern part of the Anatolian Peninsula. The Taurides are a Gondwana-derived fragment and represent an Alpine range that includes numerous tectono-stratigraphic units that piled up during the closure of the Neotethyan ocean in the Eastern Mediterranean in the Late Cretaceous to Lutetian times (Şengör and Yılmaz 1981; Göncüoğlu 1997; Göncüoğlu et al. 2004). A detailed classification of the tectono-stratigraphic units within the Taurides is suggested by Özgül (1976), who subdivided the Geyik Dağı, Bozkır, Bolkar, Aladağ, Alanya, and Antalya units, respectively. Major Alpine tectonic units of the Tauride–Anatolide Belt are shown in Fig. 1.

The Neoproterozoic basement and overlying early Palaeozoic succession are best exposed in the Geyik Dağı unit of the Central and Western Taurides. A generalized correlation of formations in the Geyik Dağı unit in the Central and Eastern Taurides is given in Fig. 2. Basement rocks are disconformably overlain by “Early Cambrian” siliciclastics of the Gögebakan Fm. and Hüdaı Fm., which are followed by carbonate rocks of the “Early” to “Middle Cambrian” Çal Tepe Fm., and subsequently by siliciclastics of the “Late Cambrian” to Ordovician Seydişehir Fm. in the Central Taurides (detailed in Gürsu and Göncüoğlu 2001; Gürsu et al. 2004).

The type section of the Çal Tepe Fm. (Fig. 3), from where the material reported here comes, is located at the Çal Tepe hill a few kilometers north of Seydişehir, at the northern side of the Taurus Mountains, southern Turkey. The stratotype was defined by Dean and Monod (1970). According to Dean and Monod (1970, 1995) and Dean (1980, 2005), the formation is divided into four members.

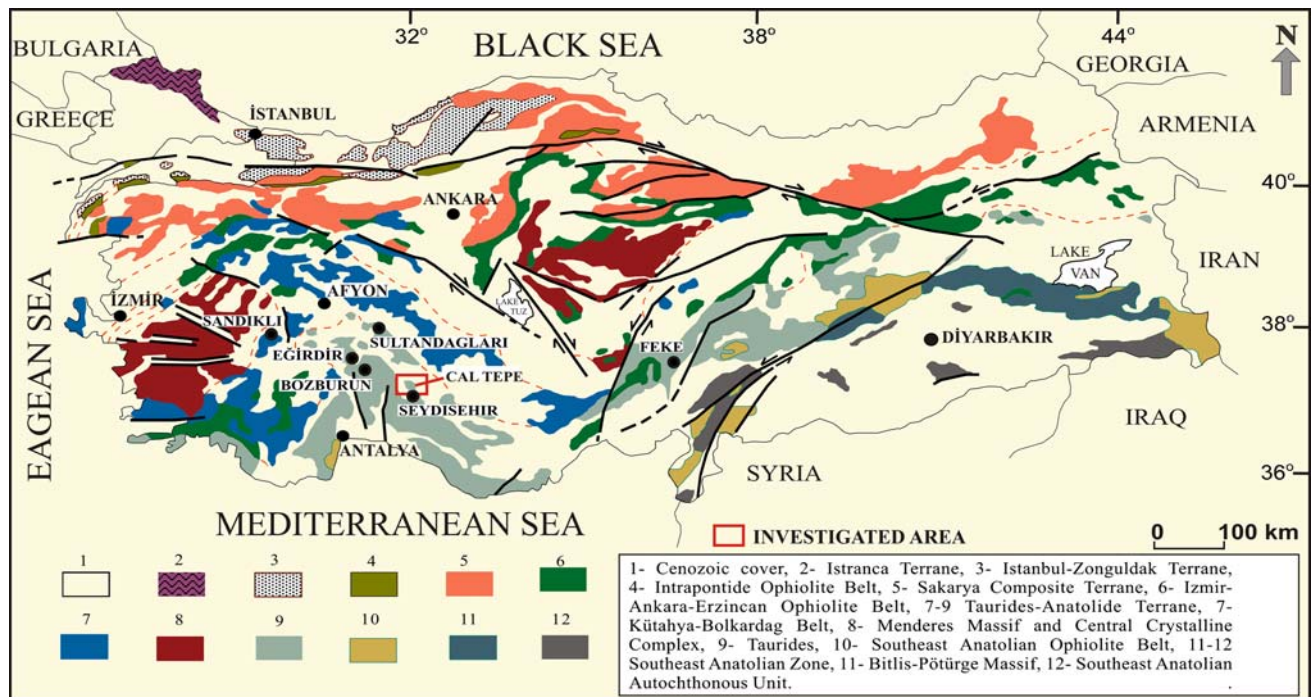


Fig. 1 Alpine tectonic units of the Tauride-Anatolite Belt of Turkey (adapted from Göncüoğlu et al. 1997)

These are in ascending order: (1) Dolomite Mbr. (more than 50 m), (2) Black Limestone Mbr. (24 m), (3) Light Grey Limestone Mbr. (about 10 m), and (4) Red Nodular Limestone Mbr. (about 47 m). The conformably overlying Seydişehir Fm. consists of shales with lenses of nodular limestone. Whereas the Dolomite Mbr. is crystalline and unfossiliferous and interpreted as supratidal to intertidal (Dean and Monod 1995), the successive Cambrian strata yield fossils and indicate transition from shallow to deep and open-marine conditions.

The stratigraphical base of the Çal Tepe Fm. is not exposed at the type locality; the Cambrian strata dip below Quaternary deposits to the northeast. Due to late Mesozoic to early Cenozoic tectonics, the whole Cambro-Ordovician succession is overturned at this site, so that the youngest horizons (“Early Cambrian”) form the top of the Çal Tepe hill (Fig. 4).

Cambrian bivalves: state of knowledge

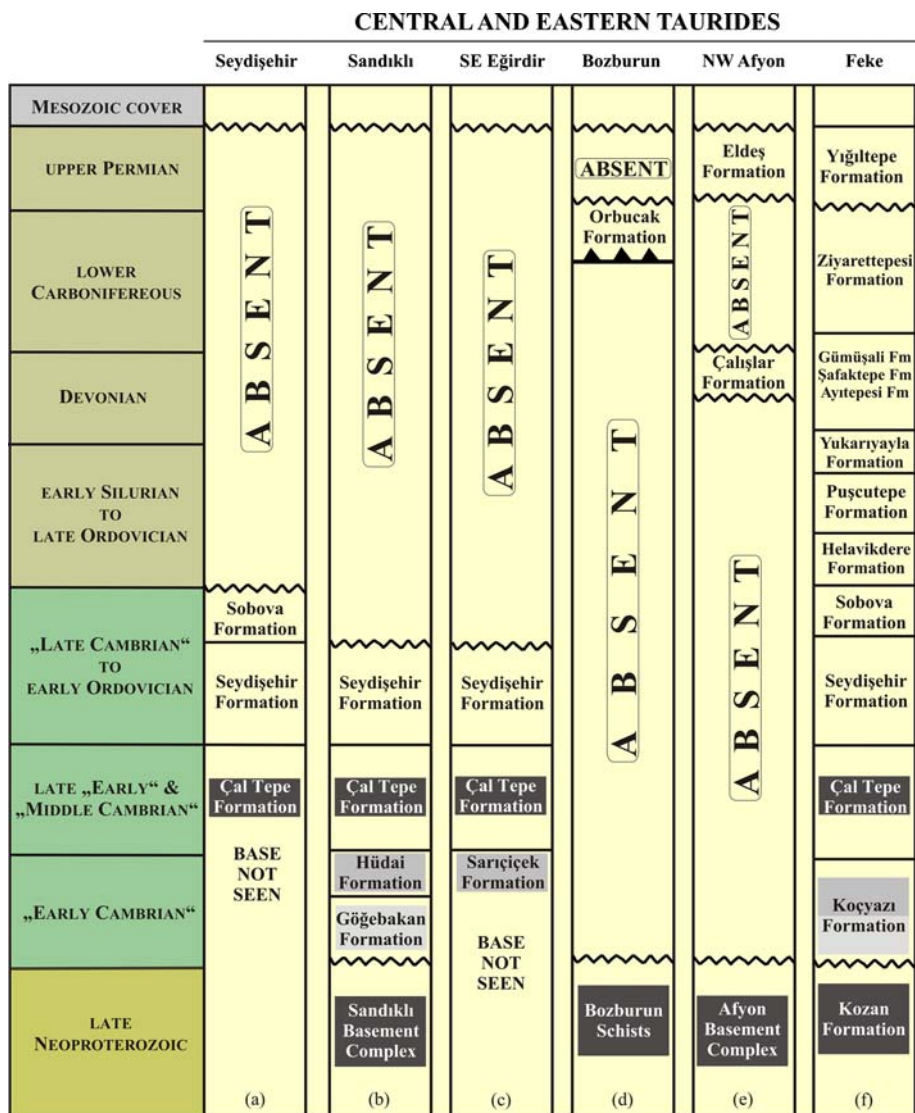
Identification of Cambrian bivalves, which have a general size of up to only a few millimeters, is often problematic because of preservation aspects. Mostly, only internal molds are available for investigation. Critical taxonomic characters are the number, position, and morphology of muscle scars, hinge arrangement, outline, and morphology of the specimens, as well as mineralogy of the shell. Definite taxonomic identification on the species level is often

problematic because of rare preservation of the first two characters. Nevertheless, if they are present in a rock sample, Cambrian bivalve steinkerns are often numerous (several 10s to more than 100 specimens) so that there is a chance to find at least a few specimens showing the needed characters.

Whereas the first Cambrian bivalve was described more than a century ago (*Fordilla troyensis* Barrande, 1881), it needed nearly 100 years until further “true” species were identified. Especially in the 1980s and 1990s a number of new taxa were introduced; 17 genera with nearly 30 species have been published, but most of them were later revised or are still problematic in their systematic affiliation (Table 1). An earlier overview was given by Pojeta (1975).

Recent investigations have confirmed a wide range of intraspecific and intrageneric variability in Cambrian bivalves (e.g., Runnegar and Pojeta 1992; Pojeta 2000; Parkhaev 2001; Skovsted 2004). Only 5 of the former 17 genera seem to represent true genera because of synonymy or systematic revisions (Table 1). Thus, for example, Geyer and Streng (1998) grouped all known species of *Pojetaia* into seven different taxa of this genus, based on shape, beaks, auricle angle, and dentition. They pointed out that only minor and remarkably small differences exist between the species. In contrast, Parkhaev (2001) investigated large samples of *Pojetaia* from different palaeogeographic regions and concluded that only three species can really be distinguished. These two examples illustrate the basic problem: limited morphological and constructional

Fig. 2 Generalized correlation charts of the Geyik Dağı unit in the Central and Eastern Taurides. Adapted from: **a** Dean and Monod (1970), Sarmiento et al. (2001). **b** Gürsu and Gönçüoğlu (2001), Gürsu et al. (2004). **c, d** Gürsu et al. (2003). **e** Gürsu and Gönçüoğlu (2008). **f** Özgül and Kozlu (2002), Monod et al. (2003)



features in Cambrian bivalves, related to the early phylogenetic stage of these organisms, combined with preservation aspects, lead to controversial concepts on the value of characters for definition of taxa at low systematic levels. For major discussions on the systematics of the Cambrian taxa and their relation to younger “true” bivalves, see Runnegar and Bentley (1983), Runnegar and Pojeta (1992), Hinz-Schallreuter (1995), Geyer and Streng (1998), Carter et al. (2000), and Pojeta (2000).

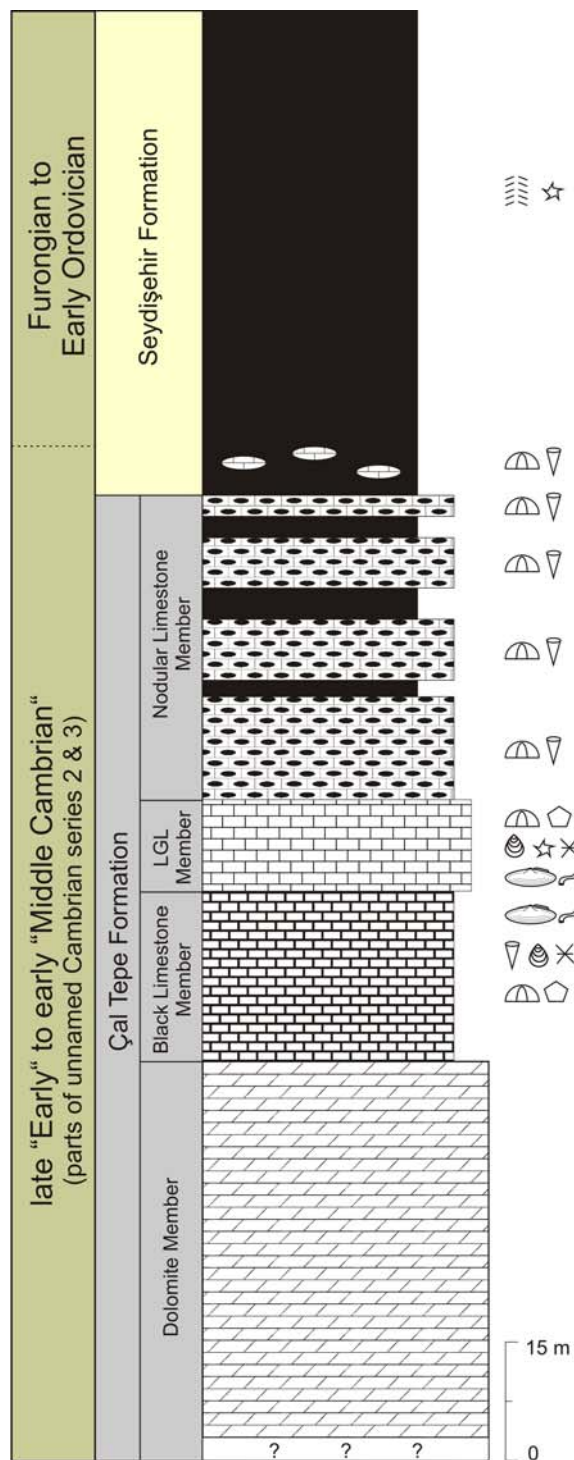
Regarding the widely accepted arguments referenced in Table 1, only five Cambrian bivalve genera can be accepted: *Fordilla* Barrande, 1881, *Pojetaia* Jell, 1980, *Tuarangia* MacKinnon, 1982, *Camya* Hinz-Schallreuter, 1995, and *Arhouria* Geyer and Streng, 1998. Additionally, *Buluniella* Jermak, 1986 is discussed and compared here because this genus—described exclusively in Russian—has mostly not been considered and is largely missing in systematic discussions.

Buluniella was introduced by Jermak (1986), who described the genus as equivalved, cryptodontic, small, very convex, opisthodetic, and roundly oval in outline. The umbo is subcentral, and the hinge margin is slightly curved. The ligament area is described as short, and the posterior adductor scar is drop-shaped. On the outer surface, growth lines and radial ribs occur. *Buluniella* is known from only one left and two right disarticulated valves from the “Early Cambrian” of Siberia. It differs from *Fordilla* in being somewhat more round in outline, in the nearly central positioned umbo, in the slightly convexity of the hinge margin (but with a straight anterior portion), and in missing a chain of muscle nodes in the anterior part of the pallial line area (Jermak 1986). From *Pojetaia* it differs in less prominent umbones (Parkhaev 2001). Regarding the high variability of characters in Cambrian bivalves (Runnegar and Pojeta 1992; Geyer and Streng 1998; Parkhaev 2001, and discussion below), the morphological features used for

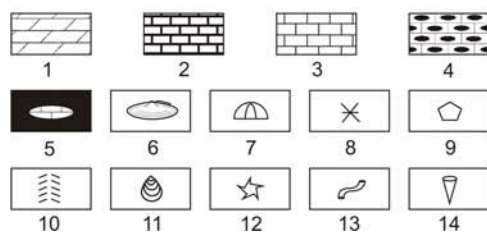
Fig. 3 Generalized columnar section of Çal Tepe Fm. at the type locality (near Seydişehir). 1 Thickly bedded, coarsely crystalline dark-grey dolomite, 2 dark-grey to black limestone, 3 light grey limestone, 4 grey pink limestone with interbeds of red nodular limestone and yellow shale, 5 green shale with limestone lenses, 6 bivalves, 7 trilobites, 8 chancelloriid and sponge spicules, 9 echinoderms, 10 trace fossils, 11 brachiopods, 12 cyanobacterial acritarchs, 13 phosphatic *small shelly fossils* (undefined), 14 undefined shell hash (modified according to Dean and Monod 1995; Sarmiento et al. 2001; Dean 2005)

separation of the genus *Buluniella* seem to be rather weak. A similar “cryptodontic” construction is also reported in the descriptions of *Fordilla*, but characteristic sigmoidal features seen in *Fordilla* in the dorsal view indicate that one more-or-less developed tooth occurs in each valve of that genus (compare Krasilova 1977, figs. 1a and 5, 6, 7; Jell 1980, figs. 2D, G; Jermak 1988, tbl. XXVII, fig. 4 and XXVIII, figs. 2, 3, 6; Boardman et al. 1987, fig. 14.112E; Elicki 1994, fig. 11; Pojeta 2000, fig. 1B; Pojeta 2007: pers. comm.; Elicki and Gürsu: herein). It is the same case in *Buluniella*. The partly missing muscle scars may be a taphonomic effect, notable in most of the Cambrian bivalve steinkerns. Runnegar and Pojeta (1992) assumed that the only known species *Buluniella borealis* belongs to *Fordilla*. We also doubt the validity of *Buluniella* as a separate genus, but the more-or-less central position of the umbo, the oval outline (figures in Jermak 1986, pl. XXV, figs. 7–9), and the remarkably small size of the specimens (1.1–1.7 mm) are typical characters of *Pojetaia*, to which genus it is referred here. Less prominent umbones (remark of Parkhaev, see above) are hardly significant because of the largely intrageneric variability of *Pojetaia* and of the poor preservation of Jermak’s few specimens. More findings and especially muscle scar preservation are needed for definite statements.

Tuarangia is known from “Middle” and “Late Cambrian” strata of eastern Gondwana and Baltica. The systematic position of this amphidetic taxon is controversial. MacKinnon (1982, 1985), Berg-Madsen (1987), and Hinz-Schallreuter (1995), mainly based on the organization of ligament and hinge (amphidetic, taxodontic, and with a ridge between the two rows of teeth) and shell microstructure (foliated calcite as in some Pteriomorphia) accepted *Tuarangia* as a true bivalve. In contrast, Runnegar (1983) and Runnegar and Pojeta (1992) interpreted the same observations another way (the occurrence of foliated calcite instead of prismatic microstructure as in true bivalves and a dorsoventral ridge do rather suggest a protoconch) and came to the interpretation of a “bivalved monoplacophoran” or a “quasiostroconch.” Pojeta (2000), referring to a not fully comprehensible reconstruction of muscle scars by Hinz-Schallreuter (1995), stated that there is no doubt of the bivalve nature of



LGL Member = Light Grey Limestone Member



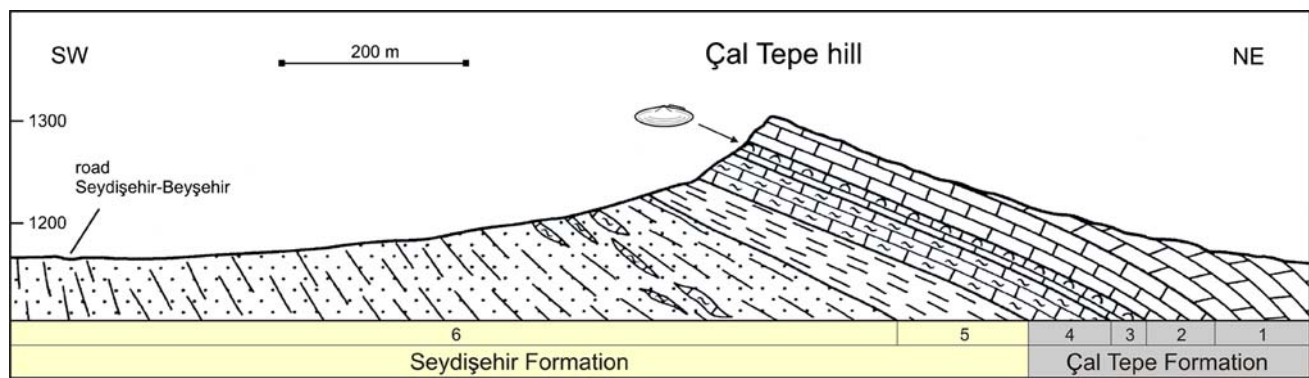


Fig. 4 Geological scheme showing the overturned Çal Tepe Fm. at the type section (near Seydişehir) and the dipping of the Cambro-Ordovician strata to the northeast. The discovery level of the bivalves is indicated (arrow). 1 Dolomite Mbr., 2 Black Limestone Mbr.,

3 Light Grey Limestone Mbr., 4 Red Nodular Limestone Mbr., 5 shale with sandstone, 6 yellow shale with limestone lenses (modified according to Dean 2005)

Tuarangia if her reconstruction is correct. So, a final systematic decision remains open until better preserved material is discovered.

Camya was defined by Hinz-Schallreuter (1995) based on two juvenile left valves from the “Middle Cambrian” *Exsulans* limestone of Bornholm (Denmark). The subtriangular shape of the valves and the distinctly anterior position of the umbo, together with the very long and straight hinge with two indistinctly pyramidal teeth (one to either side of the beak), distinguishes *Camya* from other known Cambrian bivalves. Muscle scars are not preserved. Geyer and Streng (1998) do not agree about the occurrence of any clear dentition for this taxon. Further findings and muscle scar preservation are needed also here to corroborate the systematic position of *Camya* as a bivalve.

Arhourietta was described from the early “Middle Cambrian” of Morocco by Geyer and Streng (1998). Although only two partly incomplete right valves were found and internal structures are poorly preserved, the authors describe some remarkable features of the hinge and ligament area, such as two teeth and a concave hinge plate undercutting them and posteriorly partly covered by the ligament. The authors conclude an amphidetic organization because of the occurrence of an elongate fossette anterior to umbo and teeth, interpreted as a groove of a partly internal ligament. Pojeta (2000) noted that poorly preserved imprints, interpreted by the authors as muscle scars, cannot certainly be observed on the photographs and are also not included on their reconstruction. If the interpretations by the authors are correct, then *Arhourietta* is a bivalve (Pojeta 2000) and has to be classified into the different higher systematic group of Bivalvia than the only two undoubted Cambrian bivalve genera, *Fordilla* and *Pojetaia* (see below). In contrast to this statement, at the same time Carter et al. (2000) preferred an ostracode affiliation for the holotype of *Arhourietta*.

Fordilla represents the stratigraphically earliest (early to late “Early Cambrian”) as well as the oldest described Cambrian bivalve. Based on muscle scar organization, on hinge and ligament structures, and on shell microstructure, the systematic affiliation of *Fordilla* as a true bivalve is not in doubt today. There are some common characters with *Pojetaia* in dentition and microstructure. For separation of these genera and for definition of species, the following characters are used: (1) number, position, size, and shape of muscle scars, (2) position and shape of hinge and dentition, (3) position and characters of the umbones, (4) general shape, outline, and internal and outer ornamentation, and (5) size and length-height ratio and/or length-height-width ratio. Detailed discussions about these genera have been published by Pojeta (1975), Krasilova (1977), Runnegar and Bentley (1983), Jermak (1986, 1988), Runnegar and Pojeta (1992), and Pojeta (2000). Besides the type species *Fordilla troyensis* Barrande, 1881, two further species have been introduced. *Fordilla sibirica* Krasilova, 1977, was originally described as differing from *troyensis* by showing a more rounded and somewhat smaller anterior adductor scar and a rather straight dorsal margin. *F. sibirica*, which is known from about 20 steinkerns, is a little bit broader anteriorly, but in general less concave and smaller, and does not have such distinctly radial muscles as *F. troyensis*. Runnegar and Pojeta (1992) see *F. sibirica* as lying within the range of variability of *troyensis*. *Fordilla germanica* Elicki, 1994, the third species of the genus, differs from *F. troyensis* by its slightly elongated shape, by an umbo not as strongly anterior as in *troyensis*, by the rather straight dorsal rim, and by muscle organization (Elicki 1994). The latter is very similar to that of *F. sibirica*, but *F. germanica* differs from this species by having a more elongated shape and a slightly tilted rather than a horizontal dorsal margin (Plate 3, A, B). In addition to the original description (Elicki 1994), some further remarks are given here: in the

Table 1 Cambrian taxa originally described as bivalves (in chronological order of the description of genera), their occurrence, and re-evaluated systematic affiliation

Taxon	Reported occurrence	Remarks
* <i>Fordilla</i> Barrande, 1881	“Early Cambrian” of New York, Quebec, Newfoundland, Greenland, Labrador, Bornholm, Germany, Siberia; now extended to early “Middle Cambrian” of Turkey (see text)	Pojeta (1975, 2000), Elicki (1994), Landing et al. (2002), Skovsted (2004), Elicki and Gürsu (herein); for the stratigraphic and palaeogeographic extension, see herein
* <i>F. troyensis</i> Barrande, 1881	“Early Cambrian” of New York, Quebec, Newfoundland, Greenland, Bornholm, Germany	Pojeta (1975), Elicki (1994), Landing et al. (2002), Skovsted (2004)
* <i>F. sibirica</i> Krasilova, 1977	“Early Cambrian” (Atdabanian) of Siberia	About 20 steinkern specimens; after Jermak (1986) and Runnegar and Pojeta (1992) synonymous with <i>F. troyensis</i>
* <i>F. germanica</i> Elicki, 1994	“Early Cambrian” (late Banian) of Germany	Steinkern preservation; original description extended herein (see text)
“ <i>Modiolopsis</i> ” <i>bocagei</i> Delgado, 1904	“Early Cambrian” of Portugal	<i>Modiolopsis</i> Hall 1847 is a typical Ordovician to Silurian genus with many species; Delgado erected 6 genera and 9 species from Portugal, all revised to be deformed brachiopods (Pojeta 2000)
<i>M.?</i> <i>malaisii</i> Fraipont, 1910	“Middle Cambrian” of Belgium	Revised to be a pseudofossil (Babin 1993)
<i>Davidia dollfusi</i> Delgado, 1904	“Early Cambrian” of Portugal	Deformed brachiopod (Pojeta 2000); following Carter (1971) <i>Davidia</i> Hicks, 1873 is uninterpretable and does not represent a valid genus (Kříž 2007)
<i>Lamellodonta simplex</i> Vogel, 1962	Early “Middle Cambrian” of Spain (Iberian Chains)	Deformed obolellid brachiopod (<i>Trematobolus</i>) following Havlíček and Kříž (1978), Pojeta (2000), Runnegar and Pojeta (1992)
<i>Pseudomyona queenslandica</i> (Runnegar and Jell, 1976)	“Middle Cambrian” of Australia (Queensland)	Unusual mollusk following Hinz-Schallreuter (1995); of dubious systematic affinity after Geyer and Streng (1998); no “true” bivalve after Runnegar and Pojeta (1992)
* <i>Pojetaia</i> Jell, 1980	“Early” and “Middle Cambrian” of Australia, Germany, Bornholm, Siberia, Mongolia, N-China, Morocco, NE-Greenland, ?Nova Scotia, and now also from Turkey	See for the species
* <i>P. runnegari</i> Jell, 1980	“Early” to early “Middle Cambrian” of Australia, Germany, N-China (Anhui, Henan), Transbaikalia, Mongolia, NE-Greenland, now extended to Turkey (see text)	Jell (1980), Runnegar and Bentley (1983), Li and Zhou (1986), Esakova and Zhegallo (1996), Runnegar in Bengtson et al. (1990), Elicki (1994), Parkhaev (2001), Skovsted (2004, 2006), Elicki and Gürsu (herein); following Geyer and Streng (1998) specimens (or some of them) from N-China may represent a separate species
<i>P. ovata</i> Chen and Wang, 1985	“Early Cambrian” of N-China (Henan)	Synonymous with <i>P. runnegari</i> following Runnegar and Pojeta (1992)
<i>P. elliptica</i> Li and Zhou, 1986	“Early Cambrian” of N-China (Anhui)	Synonymous with <i>P. runnegari</i> because described differences (more sub-elliptical shape and less developed auricle in “ <i>elliptica</i> ”) are in the range of intraspecific variability (discussion, see text)

Table 1 continued

Taxon	Reported occurrence	Remarks
<i>*P. ostseensis</i> Hinz-Schallreuter, 1995	“Middle Cambrian” of Bornholm	Only two left valves known; probably in the range of variability of <i>P. runnegari</i> (discussion, see text)
<i>P. sp.</i>	“Early Cambrian” of Bornholm	Berg-Madsen (1987)
<i>*P. sarthroensis</i> Geyer and Streng, 1998	Early “Middle Cambrian” of Morocco	49 steinkerns are known (discussion, see text)
<i>P.?</i> <i>terranovica</i> (Matthew, 1899)	“Early Cambrian” of Nova Scotia and SE-Newfoundland	Landing (1991), Landing and Westrop (1997)
<i>Praelamellodonta elegansa</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Genus and species refused by Geyer and Streng (1998) and Pojeta (2000); interpreted as a stenothechoid by Runnegar and Pojeta (1992)
<i>Praelamellodonta sp.</i>	“Early Cambrian” of S-China (Hubei)	Zhang (1980); refused by Geyer and Streng (1998)
<i>Xianfengoconcha</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Refused by Geyer and Streng (1998), by Qian (2001), and Pojeta (2000): may represent a brachiopod
<i>X. elliptica</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei, Guizhou)	Refused by Geyer and Streng (1998), by Qian (2001); interpreted as a stenothechoid by Runnegar and Pojeta (1992)
<i>X. rotunda</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Refused by Geyer and Streng (1998); interpreted as a stenothechoid by Runnegar and Pojeta (1992)
<i>X. elongata</i> Shu, 1986	“Early Cambrian” of S-China (Guizhou)	Refused by Geyer and Streng (1998)
<i>X. minuta</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Interpreted as a stenothechoid by Runnegar and Pojeta (1992)
<i>Cycloconchoides venustus</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Family, genus, and species refused by Runnegar and Pojeta (1992), by Geyer and Streng (1998) and Pojeta (2000): interpreted as a brachiopod or stenothechoid
<i>C. elongatus</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Interpreted as a stenothechoid by Runnegar and Pojeta (1992)
<i>Hubeinella</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Refused by Geyer and Streng (1998) and Pojeta (2000); interpreted as a brachiopod
<i>H. formosa</i> Zhang, 1980	“Early Cambrian” of S-China (Hubei)	Refused by Geyer and Streng (1998); interpreted as a stenothechoid by Runnegar and Pojeta (1992)
<i>*Tuarangia</i> MacKinnon, 1982	“Middle” to early “Late Cambrian”: New Zealand, Bornholm, Poland	Most likely a “true” bivalve (discussion, see text)
<i>T. paparua</i> MacKinnon, 1982	Late “Middle Cambrian” of New Zealand	Bivalve affinity problematic following Runnegar and Pojeta (1992)
<i>T. gravgaerdensis</i> Berg-Madsen, 1987	Late “Middle Cambrian” of Bornholm	Bivalve affinity problematic following Runnegar and Pojeta (1992)
<i>*T. gravgaerdensis tenuiumbonata</i> Hinz-Schallreuter, 1995	Late “Middle Cambrian” of Bornholm	More than 20 disarticulated valves
<i>T. sp.</i>	?late “Early Cambrian” of western Pomerania (Poland)	From ice-transported erratic boulder from Scandinavia; Berg-Madsen (1987)
<i>Oryzoconcha prisca</i> He and Pei, 1985	“Early Cambrian” of N-China (Henan)	Genus and species synonymous with <i>Pojetaia</i> respectively <i>P. runnegari</i> : Berg-Madsen (1987), Runnegar and Pojeta (1992), Geyer and Streng (1998), Parkhaev (2001)

Table 1 continued

Taxon	Reported occurrence	Remarks
<i>Yangtzedonta primitiva</i> Yu, 1985	“Early Cambrian” of S-China (Meishucun)	Genus and species accepted by Morris (1990) and Krasilova (1987), but refused as dubious microfossil by Runnegar and Pojeta (1992); problematic affiliation due to poor preservation according to Geyer and Streng (1998)
<i>Jellia</i> Li and Zhou, 1986	“Early Cambrian” of N-China (Anhui)	Synonymous with <i>Pojetaia</i> according to Geyer and Streng (1998) and Parkhaev (2001)
<i>J. elliptica</i> Li and Zhou, 1986	“Early Cambrian” of N-China (Anhui)	Synonymous with <i>P. elliptica</i> according to Geyer and Streng (1998) and Parkhaev (2001), therefore interpreted here as synonymous with <i>P. runnegari</i> (see remarks on <i>P. elliptica</i> above)
<i>J. ovata</i> Li and Zhou, 1986	“Early Cambrian” of N-China (Anhui)	Same as for <i>J. elliptica</i> (see above); following Geyer and Streng (1998) a separate new species together with special specimens, which are described as “ <i>P. runnegari</i> ” (but not corresponding to the <i>Pojetaia</i> type species) by Li and Zhou (1986)
<i>Buluniella borealis</i> Jermak, 1986	“Early Cambrian” (Tommotian) of Siberia	Genus and species known from only three valves; genus and species refused: Runnegar and Pojeta (1992) relate it to ? <i>F. troyensi</i> , and Elicki and Gürsu (herein) reassign it to <i>Pojetaia</i> (discussion, see text)
* <i>Camya asy</i> Hinz-Schallreuter, 1995	“Middle Cambrian” of Bornholm	Genus and species known from only two juvenile left valves; systematic affiliation dubious following Geyer and Streng (1998) (discussion, see text)
* <i>Arhouria opheodontoides</i> Geyer and Streng, 1998	Early “Middle Cambrian” of Morocco	Only two partly incomplete right valves known; most probably a bivalve (discussion, see text)

Taxa accepted today to be early bivalves are written in bold and indicated by an asterisk

Table 2 Important measurements on *Pojetaia runnegari* Jell, 1980

Measurements (mm) (adult specimens)	Total length	Height	Width	Anterior length (percent of the total length)
Sample T06/11-AK	1.8	1.5	0.8	1 (55.5)
Sample T06/12-AK	1.8	1.4	0.7	1 (55.5)
Sample T06/13-AK	1.6–1.9	1.3–1.4	0.6–0.8	0.8–0.9 (44.4–56.2)
<i>P. runnegari</i> (holotype)	1.1	0.8	–	0.5 (45.5)
<i>P. runnegari</i> from Germany	1.63	1.13	–	0.73 (44.7)
Further <i>P. runnegari</i>	0.93–1.04	0.64–0.75	–	0.47–0.5 (45.2–53.7)

Material from Turkey in comparison with specimens from South Australia (data from illustrations of the holotype in Jell 1980 and from illustrations in Bengtson et al. 1990)

dorsal view, the steinkern of the holotype (Plate 3, A, B; Elicki 1994, fig. 4.13) shows a sigmoidal appearance to the line between the two closed valves, indicating the occurrence of one poorly developed tooth in each valve (Plate 3, C). Such a dentition is known from both *Fordilla* and

Pojetaia (compare, e.g., Krasilova 1977; Jell 1980; Runnegar and Bentley 1983; Boardman et al. 1987; Jermak 1988; Pojeta 2000; Parkhaev 2001). The pallial muscle scars are partly connected and represent an amalgamated muscle chain. Occasionally, a pattern of polygonal cells is

Table 3 Important measurements on *Fordilla*. Material from Turkey in comparison with *F. sibirica* Krasilova, 1977 (from illustrations of the holotype in Krasilova 1977), *F. germanica* Elicki, 1994 (re-measurements on the holotype), and *F. troyensis* Barrande, 1881 (from illustrations in Pojeta et al. 1973)

Measurements (mm) (adult specimens)	Total length	Height	Width	Anterior length (percent of the total length)
Sample T06/13-AK	2.3–3.3	1.6–2.3	0.9–1.6	0.7–1.1 (29–34.8)
<i>F. sibirica</i>	2.3	1.5	–	0.8 (34.8)
<i>F. germanica</i>	3.9	2.4	1.14	1.4 (35.8)
<i>F. troyensis</i>	4.0	2.4	–	1.0 (25.0)

observed on steinkerns of *F. germanica* (Plate 3, G), corresponding to what is interpreted in *Pojetaia* as caused by an original aragonitic mineralogy (see below). Geyer and Streng (1998) have commented on the large size of *F. germanica* as indicated in the original description. Together with their interpretation of a subcentral position of the umbo and the occurrence of a small posterodorsal auricle, they came to the conclusion that *F. germanica* is better placed in the genus *Pojetaia* (“*Pojetaia germanica*”). This interpretation cannot be confirmed, and each of the counter-arguments is discussed here. The size of the holotype is given correctly in the original description. Further specimens from the same sample of the higher “Early Cambrian” strata of Germany reach a size up to 4 mm, which is not unusual in “Early Cambrian” fordillids (compare also the Turkish material described below), but is distinctly larger than any *Pojetaia* (which are around 1 1/2 mm). A more central position of the umbo in *F. germanica* is misinterpreted by Geyer and Streng (1998), especially when compared with *Pojetaia*. As originally described, the umbo is situated more central than in *F. troyensis*. However, the anterior length (horizontal distance between anterior margin and the center of the umbo) indicates that in the holotype of *F. germanica*, this distance is about 36% of the total length of the steinkern (see Table 3). In *F. sibirica* (holotype and further specimens) figured in Krasilova (1977), the anterior length is practically the same (35%). So, in both cases the umbo is more central than in *F. troyensis* where the anterior length is about 25%, but distinctly different from that of *Pojetaia* (where it is about 45–55% as measured on illustrations of specimens from Southern Australia [Bengtson et al. 1990; Alexander et al. 2001], from North-East Greenland [Skovsted 2006], and from Germany and Turkey, see Tables 2, 3). The last argument of Geyer and Streng (1998) for their revised systematic determination of *F. germanica* is the occurrence of “a small posterodorsal auricle.” Indeed, such an auricle is hitherto not explicitly described for *Fordilla*. Nevertheless, photographs by Krasilova (1977, figs. 1–3) and also by Jermak (1986, pl. XXV, figs. 2, 3) clearly show the same feature, indicating that a small auricle occurs in *Fordilla*, too, although not so pronounced as in *Pojetaia*. It

should be further noted that (1) small auricles are usually not preserved in any case and (2) that *F. sibirica* is described from only 20 steinkerns. So, the “non-occurrence” of the auricle in this long-known *Fordilla* species might be artificial. Investigation of huge numbers of steinkerns of *Fordilla* and *Pojetaia* from the Cambrian of Germany and Turkey by Elicki shows that the auricle is mostly more-or-less corroded (comp. Plate 3). So, an auricle is not a character exclusively typical for *Pojetaia*. In summary, the arguments of Geyer and Streng (1998) to reassign *Fordilla germanica* are refuted. The significant difference in size and in the position and tilting of the umbo together with the muscle arrangement indicate that *germanica* fits to the definition of the genus *Fordilla*.

Pojetaia (type species: *Pojetaia runnegari* Jell, 1980) was first reported from the “Early Cambrian” of South Australia and represents the best investigated and most reported Cambrian bivalve. The genus is known from many hundreds of specimens from Eastern and Western Gondwana, Laurentia, Baltica, and Siberia (Table 1). *Pojetaia* is equivalved and characterized by a size of about 1.5 mm and an oval to elongate outline. The ligament is opisthodontic and posterior to the more-or-less dorsocentral umbo. The latter is not tilted as in *Fordilla*. The hinge margin is slightly bent; one to three hinge teeth per valve are reported. The organization of muscle scars is similar to that of *Fordilla* (comp. Jell 1980). In *Pojetaia* the anterior adductor scar is smaller than the posterior adductor scar, but the size difference between both is not so much developed as in *Fordilla*. The pallial muscles build separate nodes more distinctly than in *Fordilla*. *Pojetaia* is known not only from steinkerns, but also with preserved shell allowing the exterior of the valves to be observed. *Pojetaia* has closely arranged growth lines and occasionally some slight radial striae. Runnegar and Bentley (1983) illustrated imbricated inclined polygonal cells on phosphatic steinkerns, which become smaller toward the margin of the valve (compare Plate 1, A, B, E). They interpreted these as impressions of the ends of prismatic aragonite fibers and one of the most distinctive features of the genus. Some years later, Runnegar and Pojeta (1992) reported very similar features present in *Fordilla troyensis* from Greenland and came to

the interpretation that this type of microstructure indicates an affiliation of *Pojetaia* and *Fordilla* in the same monophyletic group. Here, we report the same observation from *Fordilla germanica* (Plate 3, G), supporting this conclusion. As in *Fordilla*, the definition of species is sometimes problematic because of the limited number of characters and the seemingly wide range of variability of the type species (e.g., Parkhaev 2001; Skovsted 2004). There is no consensus regarding the significance of minor differences, and many newly erected species of *Pojetaia* have been synonymized later; these decisions are still controversial. Whereas Geyer and Streng (1998) mentioned six species (five species considering the re-assignment of their “*Pojetaia*” *germanica* back to the genus *Fordilla*, see discussion above), Parkhaev (2001) accepted only three valid species: *P. runnegari*, *P. ostseensis*, and *P. sarhroensis*. From our own investigations on comprehensive material from Germany and Turkey, we agree with Parkhaev’s point of view about “an extreme variability” of the type species *P. runnegari*, and we follow his conclusion of including only a few species in this genus.

According to the original designation by Hinz-Schallreuter (1995), *P. ostseensis*, which is known from only two left valves, differs from *runnegari* by a little larger size (of about 25%) and a somewhat higher shell, as well as by the occurrence of three teeth in the left valves. Parkhaev (2001) mentioned a less distinct posterodorsal angle than in *runnegari*. However, considering the variability of *P. runnegari* and the very limited number of specimens known of *P. ostseensis*, the two-first mentioned differences are not significant. Accepting this, the number of teeth would represent the only new character of *P. ostseensis* but, as already noted by Hinz-Schallreuter, Jell (1980) mentioned up to three teeth for *P. runnegari* in his original designation. Consequently, this character is in the range of variability of *P. runnegari*, too, and the introduction of the taxon *P. ostseensis* cannot be justified. The only notable difference to *P. runnegari* seems to be in the larger auricle angle.

Geyer and Streng (1998) introduced the species *Pojetaia sarhroensis* based on 50 internal molds from the early “Middle Cambrian” of the Moroccan Anti-Atlas. Emphasizing that differences between all the species of that genus are very small, the authors pointed out that *P. sarhroensis* resembles the type species *P. runnegari* in most respects; differences include a smaller and less pronounced posterior auricle, very low umbones, a larger auricle angle, the “occasionally” higher number of teeth (up to four), and the larger posterior tooth. Whereas the two first-mentioned characters may be in the range of variability of *P. runnegari*, the other characters are distinctive.

P.? *terranovica* (Matthew, 1899) is mentioned by Landing and Westrop (1997). The taxon is briefly

described by Landing (1991) as *Watsonella?* *terranovica* (Matthew, 1899). He suggests similarity to *W. crosbyi* Grabau, 1900, but refers to a prominent radial posterior sulcus as a difference. He concluded that *W.?* *terranovica* may be a rostroconch and referable to *Watsonella*, or a bivalve. So, the systematic position of this taxon is still problematic.

In summary, it can be stated that two Cambrian genera can be accepted as undoubtedly representing early Bivalvia: *Fordilla* Barrande, 1881, and *Pojetaia* Jell, 1980 (for general phylogeny of these early bivalves, see references given above). Considering the large range of intraspecific variability that has become recognized in recent years, three species of the first (*F. troyensis* Barrande, 1881, *F. sibirica* Krasilova, 1977, *F. germanica* Elicki, 1994) and two, but probably three of the latter (*P. runnegari* Jell, 1980, *P. sarhroensis* Geyer and Streng, 1998, and probably *P. ostseensis* Hinz-Schallreuter, 1995) represent valid species.

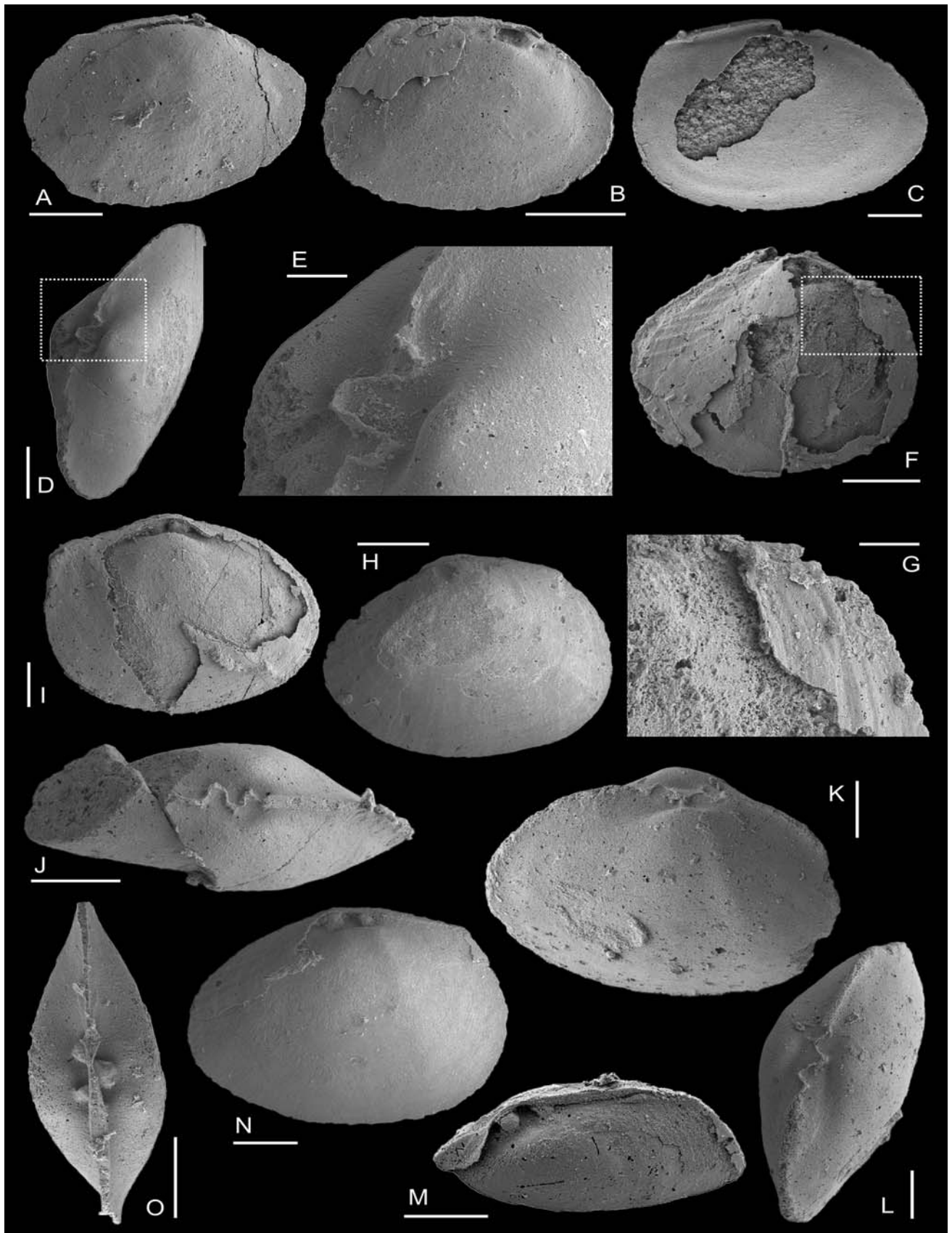
Three further genera most likely represent Bivalvia: *Tuarangia* MacKinnon, 1982 (including two species and one sub-species), *Camya* Hinz-Schallreuter, 1995 (including only the type species), and *Arhourliella* Geyer and Streng, 1998 (including only the type species). The question marks on the determinations of their systematic affiliation are due to the sometimes poor preservation of critical characters combined with the very limited number of specimens hitherto known.

Cambrian Bivalvia from Turkey

Preservation, stratigraphic position, and lithofacies

The bivalve remains from Turkey were extracted by chemical preparation using diluted formic and acetic acids. They are preserved as blackish phosphatic steinkerns (Plates 1, 2). Rarely, some light shell remains are visible (Plate 1, B, C, F–I, N). Specimens are generally articulated, but the steinkerns are often sheared due to the local tectonic situation (Plate 1, J). More than 150 specimens were obtained from samples of about 8 kg. In addition, the tectonically sheared specimens produced a lot of fragments because of the chemical preparation procedure. Muscle scars are rarely preserved, and often they are only faintly visible under a light microscope. Radiating striae and growth lines are preserved on several specimens and are described below.

The rock samples from which the vast majority of microfossils were extracted come from the lowermost portion of the Light Grey Limestone Mbr. of the Çal Tepe Fm. at its type locality (Fig. 3). The sampled lithostratigraphic interval corresponds approximately to the higher *Acadoparadoxides mureroensis* biozone (Iberian scale) or to the

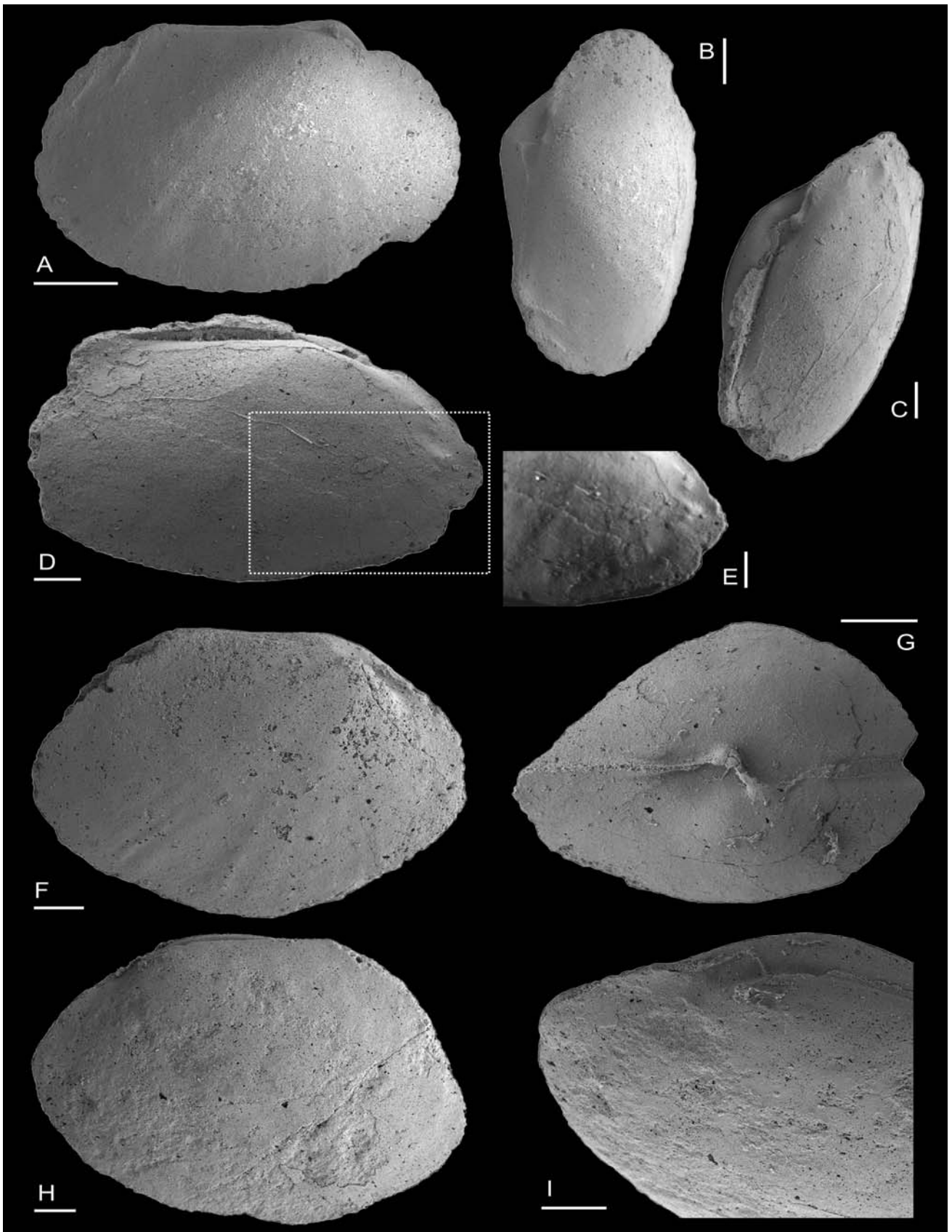


◀ **Plate 1** *Pojetaia runnegari* Jell, 1980. SEM micrographs. All specimens from Çal Tepe type section. Specimen shown in **K** and **L** come from upper Black Limestone Mbr.; all others are from lower Light Grey Limestone Mbr. Thread-like structures on some specimens are due to contamination during the coating procedure and do not represent microbial overgrowths. **A** Right lateral view of specimen FG600_OT55-7. Note the slightly elongated shape and the polygons on the surface of the steinkern interpreted as pointing to a primary aragonite mineralogy (see text), visible near the ventral margin. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **B** Right lateral view of specimen FG600_OT240-5. Note the polygonal cells in the lower half of the picture, the cells are getting closer near the ventral margin. Two hinge teeth are visible. Shell remains at the posterior auricle are phosphatic and show dense growth lines. Phosphatic steinkern partly with pseudomorphic shell preservation; sample T06/13-Ak; scale bar: 0.3 mm. **C** Right lateral view of specimen FG600_OT55-2. Nearly complete phosphatic (pseudomorphic) shell preservation with phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **D** Dorsal, inclined view of specimen FG600_OT240-4. Posterior end is pointing down. Area indicated by rectangle is illustrated in **E**. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **E** Enlarged view of the hinge area of the specimen shown in **D**. Dentition shows traces of one tooth in the right valve and two teeth in the left valve. Note further the traces of the polygonal microstructure of shell prisms (compare to **A** and **B**). Scale bar: 0.1 mm. **F** Left lateral view of specimen FG600_OT55-4. Faint ribs are restricted to the anterodorsal region. In the same area close growth lines are clearly visible. Two teeth are poorly preserved. Area indicated by rectangle is illustrated in **G**. Phosphatic steinkern with phosphatic (pseudomorphic) shell preservation; sample T06/13-Ak; scale bar: 0.3 mm. **G** Enlarged view of the posterodorsal edge of specimen shown in **F**. Note the very close growth lines. Scale bar: 0.1 mm. **H** Left lateral view of specimen FG600_OT55-6. Note very close growth lines of a rather thin shell pseudomorph. Phosphatic steinkern with nearly complete phosphatic shell preservation; sample T06/13-Ak; scale bar: 0.3 mm. **I** Right lateral view of specimen FG600_OT55-5. Note the co-marginal growth lines, the distinct posterodorsal auricle, and two hinge teeth. Phosphatic steinkern with partial preservation of phosphatic shell pseudomorph; sample T06/13-Ak; scale bar: 0.3 mm. **J** Dorsal view of specimen FG600_OT240-16. Type of dentition as in **E** (specimen FG600_OT240-4); ligament space is filled with sediment. The specimen has been sheared by younger tectonics (and healed again), which is quite often in the investigated material. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **K** Left lateral, inclined view of specimen FG600_OT586-1. Note faint ridge running from the left umbo to the posteroventral area. Phosphatic steinkern; sample T06/11-Ak; scale bar: 0.3 mm. **L** Dorsal view of the same specimen as shown in **K**. Anterior end is pointing down. Note the type of dentition: one tooth in the right valve, two teeth in the left. Scale bar: 0.3 mm. **M** Left lateral view of the posterodorsal area of specimen FG600_OT240-6. One tooth and two sockets are visible. Ligament shows layered construction. Phosphatic steinkern with partial preservation of phosphatic shell; sample T06/13-Ak; scale bar: 0.3 mm. **N** Left lateral view of specimen FG600_OT240-12. Note two faint ridges running from the left umbo to the ventral margin: the left one of both is very weakly developed. On the shell remains of anterodorsal area ribs and close growth lines are visible (compare to **F**). Phosphatic steinkern with partial preservation of phosphatic shell; sample T06/13-Ak; scale bar: 0.3 mm. **O** Dorsal view of specimen FG600_OT240-7. Posterior end of the specimen is pointing down. Ligament is lenticular and ligament space is filled with sediment. Hinge teeth are transposed in this specimen compared, e.g., with specimens shown in **D** and **J**. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm

higher *Cephalopyge notabilis* biozone (Moroccan scale). Depending on the stratigraphic concept used, this biostratigraphic level belongs to the earliest “Middle Cambrian” (Sdzuy et al. 1999; Dean 2005) or to a little younger early “Middle Cambrian” (Geyer and Landing 2004). Following the intentions of the new stratigraphic subdivision of the Cambrian system by the *International Commission on Stratigraphy*, these biozones correspond to the first stage of “series 3” of the Cambrian, both unnamed so far. A latest “Early Cambrian” age for the lower portion of the Light Grey Limestone Mbr. was assumed by Sarmiento et al. (2001) based on a *small shelly fossil* assemblage from a level of about 1 m above the base of the member and, from personal communication, on the lowest occurrence of “Middle Cambrian” trilobites from a level of about 1.80 m above the base, given by Dean and Monod in 1995. However, more recent work on trilobites of the Çal Tepe type section published by Dean (2005) led to findings of paradoxid remains 0.40 m above the base of the Light Grey Limestone Mbr., indicating that only the first few centimeters, at best, might be of latest “Early Cambrian” age. So, the traditional “Early–Middle Cambrian” boundary (in the sense of Sdzuy et al. 1999; Dean 2005) is nearly coeval to the transition from the Black Limestone Mbr. to the Light Grey Limestone Mbr. (Dean 2005).

Only three more-or-less fragmented bivalve specimens come from a few meters below this level (upper Black Limestone Mbr.) and are assigned to the *Protolenus* (*Hupeolenus*) biozone (Sdzuy et al. 1999; Dean 2005) or the *Hupeolenus* biozone (Geyer and Landing 2004), which means at the latest “Early Cambrian” in the sense of the former, but earliest “Middle Cambrian” in the sense of the latter.

The limestone samples from which the bivalves are reported represent different lithofacies types. The sample from the Black Limestone Mbr. (sample no. T06/11-Ak) is a bioturbated peloidal pack- to grainstone with some fossil content (mostly disarticulated cancelloriids and echinoderms). In contrast, the majority of bivalves (more than 95%) comes from two bioclastic limestones of the Light Grey Limestone Mbr.: (1) a few specimens were found in an echinoderm wacke- to packstone (sample no. T06/12-Ak) together with trilobites, brachiopods, poriferids, and hyoliths (facies type 1). Most of these bioclasts are relatively large so that this lithotype is sometimes close to floatstone, (2) nearly all of the specimens from the Light Grey Limestone Mbr. are from a bioclastic wackestone (sample no. T06/13-Ak) rich in disarticulated cancelloriids and echinoderms, accompanied by poriferids, hyoliths, “gastropods,” trilobites, brachiopods, and some *small shelly fossils* (facies type 2). Although echinoderms are not rare in this lithotype, they do not reach such a distinct



◀ **Plate 2** *Fordilla* sp. SEM micrographs, with exception of E. All specimens from lower Light Grey Limestone Mbr. of Çal Tepe type section. Thread-like structures on some specimens are due to contamination during coating procedure and do not represent microbial overgrowths. **A** Right lateral view of specimen FG600_OT125-3. Note the distinctly more anterior position of the umbo compared with *Pojetaia*. Faint radial ribs are clearly visible. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **B** Dorsal, inclined view of the same specimen as in **A**. Posterior end is pointing down. Note the traces of one poorly developed tooth in each valve, leading to a sigmoidal line dorsally. Phosphatic steinkern; scale bar: 0.3 mm. **C** Dorsal, inclined view of specimen FG600_OT125-10. Posterior end is pointing down. Posterodorsally, remains of the ligament and of an auricle can be observed. Ligament space is filled with sediment. Hinge construction as in specimen FG600_OT125-3 (**A**, **B**). Near the anterior margin, few and poorly preserved muscle scars occur (compare **D** and **E**). Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **D** Right lateral view of the same specimen as in **C**. Some shell remains are preserved dorsally and anteriorly. The area indicated by rectangle is illustrated in **E**. Scale bar: 0.3 mm. **E** Light-microscopic micrograph of the anteroventral area of the specimen shown in **C** and **D**. Few indistinct scars of some pallial muscles and of the anterior adductor are visible. Scale bar: 0.3 mm. **F** Right lateral view of specimen FG600_OT125-11. Note the very anterior position of the umbo and the radial ribs. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **G** Dorsal view of specimen FG600_OT125-9. Note the traces of poorly developed hinge teeth leading to a sigmoidal line dorsally. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **H** Left lateral view of specimen FG600_OT125-12. Anterior is to the left. Note the very anterior position of the umbo and the large size of this incomplete specimen. Phosphatic steinkern; sample T06/13-Ak; scale bar: 0.3 mm. **I** Enlarged view of the hinge area of the specimen shown in **H**, showing the typical sigmoidal line. Scale bar: 0.3 mm

majority as in the other sampled limestones of this member (facies type 1). Additionally, the bioclasts are clearly thinner and smaller in facies type 2.

An interesting observation is the occurrence of idiomorphic bipyramidal quartz crystals, which occur in each of the samples in large numbers. The crystals are long, prismatic, and measure up to 1 mm in length. Investigations using cathodoluminescence microscopy led to identification of calcite inclusions within the crystals, pointing to an authigenic origin by replacement of the carbonate during diagenesis. Crystal surfaces are slightly etched by subsequent diagenetic corrosion. The source of the silica might be related to diagenetic mobilization from nearby Mesozoic radiolarites and/or volcanics or to early Cenozoic volcanic processes known from the area. This diagenetic aspect will be the subject of a separate investigation.

Systematic palaeontology

The higher systematic affiliation of Cambrian bivalves is discussed in varying degree in Pojeta (1975), Runnegar and Bentley (1983), Runnegar and Pojeta (1992),

Hinz-Schallreuter (1995), Geyer and Streng (1998), Carter et al. (2000), and Schneider (2001) and is not repeated here.

Class Bivalvia Linnaeus, 1758

Order uncertain

Family Fordillidae Pojeta, 1975

Genus *Pojetaia* Jell, 1980

*1980 *Pojetaia* Jell: 234–237.

1985 *Oryzoconcha* He and Pei—He and Pei: 63.

1986 *Jellia* Li and Zhou—Li and Zhou: 36.

1986 *Buluniella* Jermak—Jermak: 186.

1990 *Pojetaia* Jell—Bengtson et al.: 256.

2001 *Pojetaia* Jell—Parkhaev: 200.

Type species: Pojetaia runnegari Jell, 1980, figs. 2A–B; “Early Cambrian”, Parara Limestone, South Australia

Diagnosis Tiny bivalve (less than 2 mm), subequivalved, suboval to slightly elongated; umbo central to subcentral and prosogyral; ligament straight and opisthodontic-parivincular; dentition is of one to three teeth (one to two in each valve); posteriorly a more-or-less developed auricle; externally fine comarginal growth lines and faint ribs dorsoanteriorly; small anterior adductor muscle, posterior adductor muscle sizeable, pallial muscles arranged comarginally as a series of discrete nodes.

Remarks For stratigraphic and geographic distribution, see Table 1 and Fig. 5.

Composition The genus includes two, probably three species: *P. runnegari* Jell, 1980, *P. sarthroensis* Geyer and Streng, 1998, and probably *P. ostseensis* Hinz-Schallreuter, 1995 (see discussion above).

Pojetaia runnegari Jell, 1980

(Plate 1, A–O)

*1980 *Pojetaia runnegari* Jell: figs. 1, 2, 3C–K.

1983 *Pojetaia runnegari* Jell—Runnegar: fig. 10.

1983 *Pojetaia runnegari* Jell—Runnegar and Bentley, figs. 1, 3, 4, 6A, B, D, E, 7A, B, D, G.

1985 *Pojetaia ovata* Chen and Wang—Chen and Wang: 28.

1985 *Pojetaia runnegari* Jell—He and Pei: pl. 1, figs. 1, 3, 4.

1985 *Oryzoconcha prisca* He and Pei—He and Pei: pl. 1, figs. 2, 5, pl. 2, figs. 1–3.

1986 *Jellia elliptica* Li and Zhou—Li and Zhou.

1986 *Jellia ovata* Li and Zhou—Li and Zhou.

1986 *Pojetaia elliptica* Li and Zhou—Li and Zhou.

1986 *Buluniella borealis* Jermak—Jermak: pl. XXV, figs. 7–9.

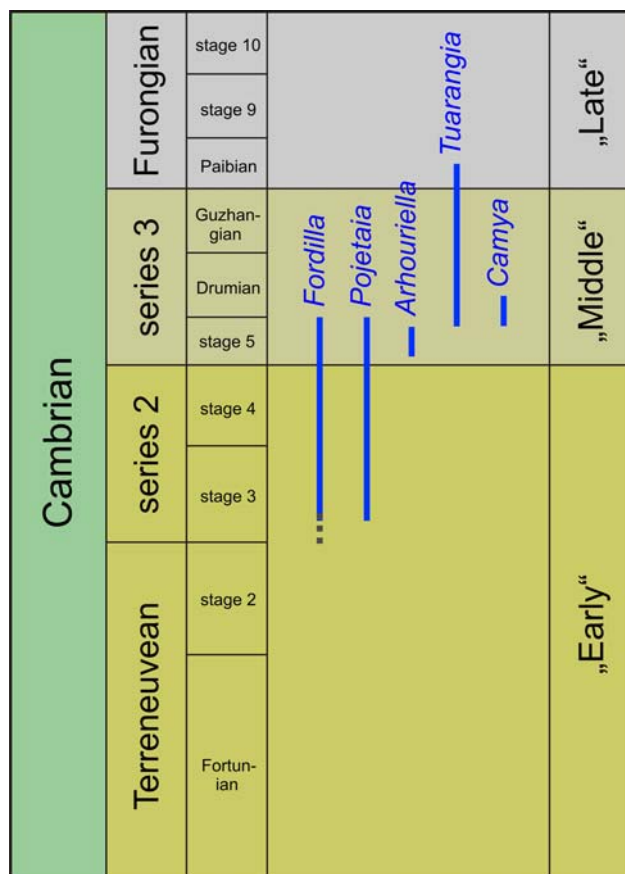


Fig. 5 Stratigraphic range of Cambrian bivalves (for discussion see text)

1987 *Pojetaia runnegari* Jell—Yu, pl. 68, figs. 9–14.

1990 *Pojetaia runnegari* Jell—Bengtson et al., figs. 165–166.

1994 *Pojetaia runnegari* Jell—Elicki, fig. 4.14.

?1995 *Pojetaia ostseensis* Hinz-Schallreuter—Hinz-Schallreuter, figs. 4.1–4.2.

1996 *Pojetaia runnegari* Jell—Esakova and Zhegallo: pl. XXIII, figs. 8–14.

2000 *Pojetaia runnegari* Jell—Elicki, pl. 1, fig. 9.

2001 *Pojetaia runnegari* Jell—Parkhaev, pl. XLIX and L.

2004 *Pojetaia runnegari* Jell—Skovsted, figs. 9a–f.

Holotype Jell (1980), figs. 2A–B, National Museum of Victoria collection number P59669.

Material About 80 articulated phosphatic internal molds and numerous fragments; rare pseudomorphic phosphatic shells; one specimen and three fragments from the upper Black Limestone Mbr. (sample T06/11-Ak), late “Early Cambrian”; all other remains from lower Light Grey Limestone Mbr. (T06/12-Ak and T06/13-Ak), early

“Middle Cambrian”; all specimens from Çal Tepe Fm., Çal Tepe hill, Western Taurides, Turkey.

Description Tiny bivalves (1.6–1.9 mm), equivalved, suboval in outline to slightly elongated posteriorly. Umbones are mostly, but not in every case prominent; if prominent, then very faint radial ridges may run left and right of the umbo to the ventral margin (Plate 1, G). The umbones are located more-or-less central at 44–56% of the total length to the anterior margin (anterior length; Table 2, Fig. 6). Passing of the slightly convex ventral margin to the anterior and posterior margins is gentle; transition to the dorsal margin by a distinct bend. Posteriorly, a more-or-less prominent auricle is developed (Plate 1, A–C, I, N). Dorsal margin is straight. The long ligament is lenticular, externally (parivincular), and behind the umbo (opisthodontic). The hinge has one or two relatively small teeth in each valve and corresponding sockets (Plate 1, B, D, E, I–O). Transposition of hinge teeth can be observed. Muscle scars are only rarely preserved on the steinkerns. A small and elongated anterior adductor, and in the anterior region of the mold some very faint comarginal arranged scars of pallial muscle nodes (roundly to slightly elongated towards the umbo) could very rarely be observed under light microscope. Internally (on steinkern surfaces), small irregular polygons, becoming smaller towards the valve margin, occur (Plate 1, B, E). Externally, when pseudomorphic shell preservation is present, close and faint comarginal growth lines and anterodorsal low ribs are visible (Plate 1, B, F–I).

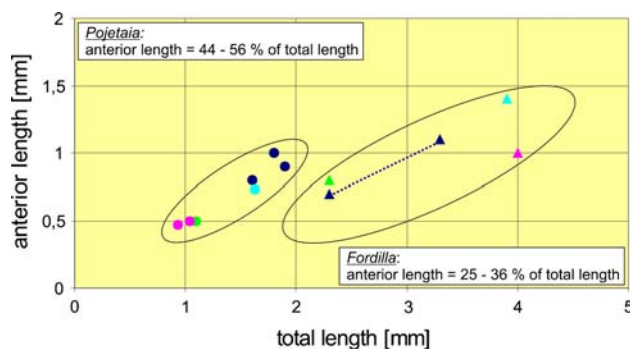


Fig. 6 Ratio of anterior length to total length in *Fordilla* and in *Pojetaia* (compare also Tables 2, 3). Note that the values are significantly larger in *Pojetaia*, which means that the umbo is generally more central (positioned between 44 and 56% of the total length of the specimens). Circles *Pojetaia runnegari* Jell, 1980 (pink specimens from S-Australia; green holotype; light-blue specimens from Germany; dark-blue specimens from Turkey); triangles *Fordilla* (pink holotype of *F. troyensis* Barrande, 1881; green holotype of *F. sibirica* Krasilova, 1977; light-blue holotype of *F. germanica* Elicki, 1994; dark-blue: *F. sp.* from Turkey [dotted line indicates the range of all Turkish specimens])

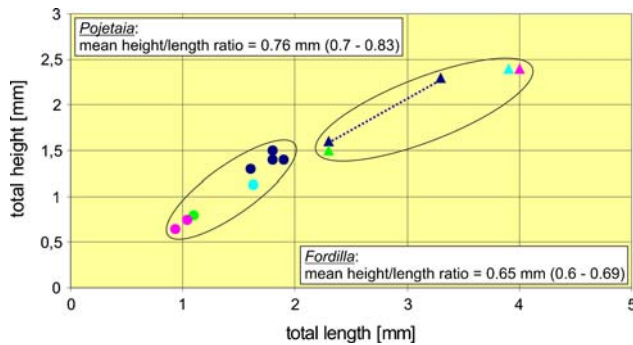


Fig. 7 Height-length ratio in *Fordilla* and in *Pojetaia* (compare also Tables 2, 3). The values are distinctly smaller in *Fordilla*, which means that the outline is generally more elongated. But note that the values in some *Fordilla* from Turkey and in the holotype of *F. sibirica* Krasilova, 1977, are relatively close to values in some of the *Pojetaia* specimens from Turkey; this indicates that the general outline alone is not a sufficient character for a systematic separation of both genera. Symbols as for Fig. 6

Remarks The specimens from Turkey seem to have a relatively wide range of variability as already reported elsewhere (see discussion above). This includes the shape, the prominence of umbones and auricle, and the size. The latter falls in a range characteristic for the genus (compare Table 2). Besides the total size of the specimens, further useful data include the percentaged anterior length, which gives the position of the umbo relative to the total length of the specimen and in the total height to length ratio. The first is 44.4–56.2%, which is consistent with data from the holotype (Table 2; Fig. 6) and distinctly different from that of *Fordilla* (see Table 3; Fig. 6). The total height to length ratio ranges from 0.7 to 0.83 (Fig. 7) and indicates a somewhat oval outline, but is near to *Fordilla* in its smaller values (see below). This means that the outline alone is not a good taxonomic characteristic. In contrast, the absolute values of the total length of *Pojetaia* differ significantly from that of *Fordilla*, which is distinctly larger. The given measurements are comparable to those published by Parkhaev (2001).

Genus *Fordilla*, Barrande, 1881

1881 *Fordilla* Barrande: 342.

1977 *Fordilla* Barrande—Krasilova: 45.

Type species: *Fordilla troyensis* Barrande, 1881, “Early Cambrian”, New York State

Diagnosis Small equivalved bivalve (up to 4 mm); laterally compressed, posteriorly somewhat broadened, sub-oval valves; anterior adductor smaller and more developed than posterior adductor, pallial line integripalliate and posteriorly widened, pallial line anteriorly as a ridge of

several connected nodes which are slightly elongated to the umbo, small pedal retractor muscle scar dorsal to the anterior adductor scar, one to two dorsoumbonal muscle scars below the umbo; umbo small and located anteriorly, beakes prosogyral; hinge straight or somewhat convex, one tooth in each valve; externally close comarginal growth lines and occasional faint ribs.

Remarks For stratigraphic and geographic distribution, see Table 1 and Fig. 5.

Composition The genus includes three species: *F. troyensis* Barrande, 1881, *F. sibirica* Krasilova, 1977, and *F. germanica* Elicki, 1994 (see discussion above).

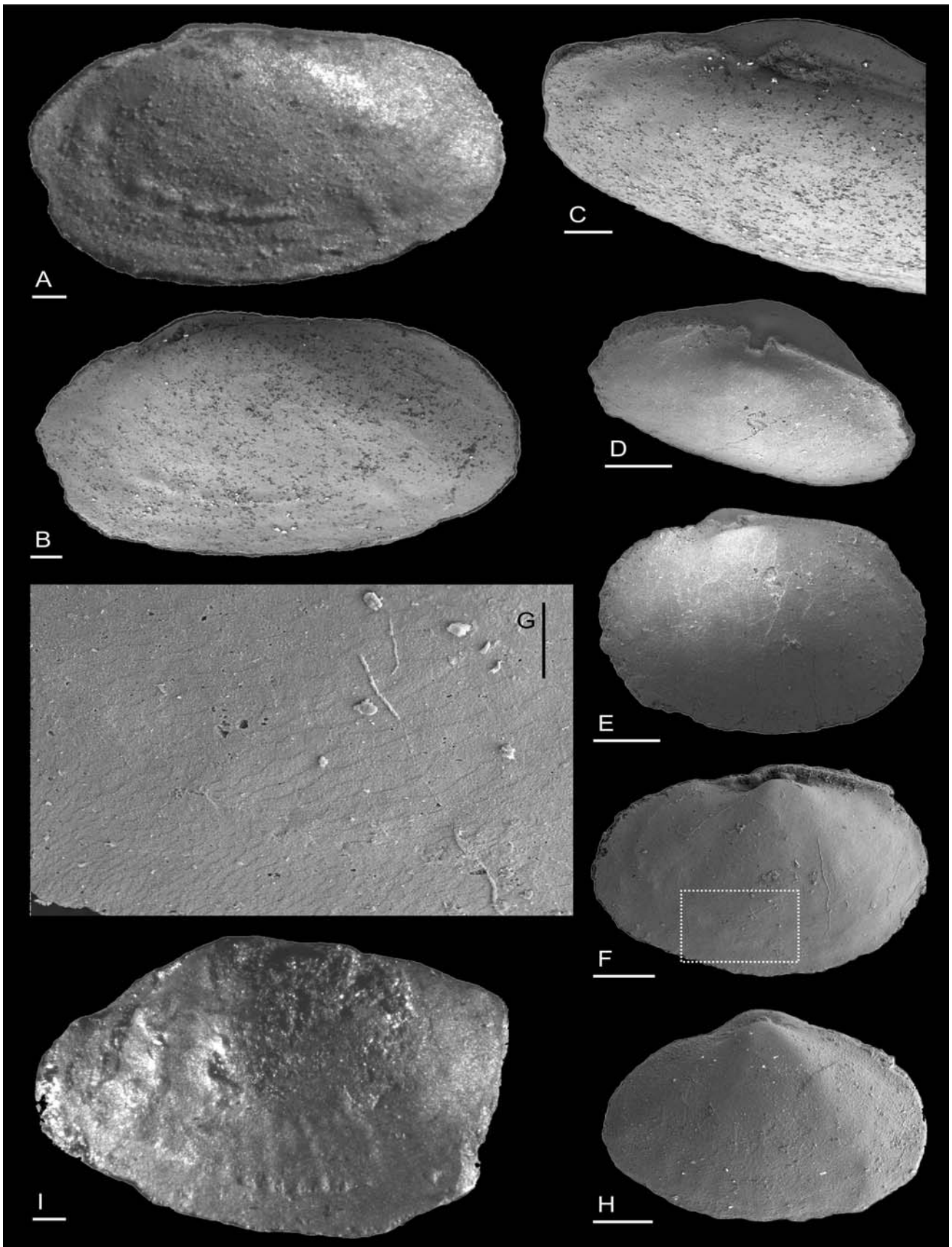
Fordilla sp.

(Plate 2, A–I)

Material Ten articulated and partly fragmented phosphatic internal molds of mostly adult and few juvenile specimens from the lower Light Grey Limestone Mbr. (T06/13-Ak), early “Middle Cambrian”, Çal Tepe Fm., Çal Tepe hill, Western Taurides, Turkey.

Description The bivalve is small (adults: 2.3–3.3 mm), but distinctly larger than *Pojetaia* from the same sample in both total length and width (Table 3). *Fordilla* sp. is sub-oval. Anteriorly, a small adductor muscle scar and a smaller pedal muscle scar above are sometimes visible on the steinkern (Plate 2, C–E). Pallial muscles seem to have built a rather amalgamated and not fully co-marginal string, but on one steinkern some node-like pallial muscle scars could be observed (Plate 2, E). Additional muscles scars are not preserved. The umbo is located anteriorly (percentaged anterior length of 29–35%, Table 3, Fig. 6) and tilted. Hinge is straight to slightly convex and shows sockets of one poorly developed tooth in each valve leading to a sigmoidal line dorsally (Plate 2, B, C, G, I). Posterodorsally, remains of an auricle are visible (Plate 2, A–D). Faint radial ribs are visible on some steinkerns (Plate 2, A, F).

Remarks Originally, *Fordilla* (*F. troyensis*) was described as without true anterior and posterior teeth (e.g., Pojeta 1975). Krasilova (1977) described *Fordilla sibirica* as cryptodontic, too, but on the figured specimens a typical sigmoidal dorsal running of the line between the valves can be observed. The same is the case on the specimens figured in Boardman et al. (1987) and Pojeta (2000). This distinct sigmoidal course (well visible on nearly each steinkern) points to the occurrence of one rather poorly developed tooth in each valve. The size range of the specimens as well as the tilting and position of the umbo are characteristic. The



◀ **Plate 3** *Fordilla germanica* Elicki, 1994, *Fordilla troyensis* Barrande, 1881, and *Pojetaia runnegari* Jell, 1980. SEM micrographs, with exception of **A** and **I**. All specimens from the Upper Ludwigsdorf Mbr. (Charlottenhof Fm., late Early Cambrian) of the Görlitz Synclinorium (Germany). **A** Left lateral view of *Fordilla germanica* Elicki, 1994; holotype; light-microscopic micrograph. Note the scars of anterior pallial muscles, which consist of three slightly connected, but distinguishable nodes (anteriorly). Near the anterior margin, a larger and drop-shaped muscle field (anterior adductor and anterior pedal retractor muscles) can be seen. A very faint dorsomedian muscle and arguable posterior muscles seem to occur on further steinkerns (see original description in Elicki 1994). Posteriorly, some faint radial ribs occur. Phosphatic steinkern; sample L22/23; scale bar: 0.3 mm. **B** SEM micrograph of the same specimen as in **A** and **C**, in left lateral view. Posteriorly, a poor extension of an auricle can be seen. Scale bar: 0.3 mm. **C** Same specimen as in **A** and **B**, showing the hinge area with the typical sigmoidal line, indicating the occurrence of one poorly developed tooth in each valve. In contrast to *Pojetaia*, no other type of dentition is known from this genus. Scale bar: 0.3 mm. **D** Dorsal, inclined view of *Pojetaia runnegari* Jell, 1980 (specimen FG600_OT204-5). Posterior end is to the right. Note the difference compared to *Fordilla* in the type of dentition and in the central position of the umbo. Phosphatic steinkern; sample L22/23; scale bar: 0.3 mm. **E** Left lateral view of the same specimen as in **D**. Note the distinct posterior auricle. Scale bar: 0.3 mm. **F** Left lateral view of *Pojetaia runnegari* Jell, 1980 (specimen FG600_OT204-6). Posterior end is to the right. The surface of the steinkern is marked by the boring microbe *Endoconchia lata* Runnegar, 1990. Polygons on the steinkern point to a primary aragonite mineralogy (compare to Plate 1, **A**, **B**, **E**, see text). Area indicated by rectangle is illustrated in **G**. Phosphatic steinkern; sample L22/23; scale bar: 0.3 mm. **G** Enlarged view of the indicated area of the specimen shown in **F**. Note the polygonal cells which become distinctly smaller to the ventral margin. The small threads represent the boring microbe *Endoconchia lata* Runnegar, 1990. Scale bar: 0.1 mm. **H** Left lateral view of *Pojetaia runnegari* Jell, 1980 (specimen FG600_OTGSyVI-1). Posterior end is to the right. As in this specimen, the posterior auricle is often largely abraded. Phosphatic steinkern; sample L22/23; scale bar: 0.3 mm. **I** Left lateral view of *Fordilla troyensis* Barrande, 1881 (figured in Elicki 1994, Fig. 4.12). Note the elongated pallial muscle scars and the relatively large anterior muscle field. The umbo is more anterior than in other species of the genus or in *Pojetaia*. Phosphatic steinkern; sample L22/23; scale bar: 0.3 mm

latter is located anteriorly at a distance to the anterior margin of one-third of the total length of the steinkern (Table 3; Fig. 6). Comparison with the data of the holotypes of *F. sibirica* and *F. germanica* shows that all three species of the genus correspond in these characters and are very different to *Pojetaia*. The height-length ratio of all the Çal Tepe specimens is between that of the holotypes of *F. troyensis*, *F. sibirica*, and *F. germanica*, and of that of *Pojetaia* (Tables 2, 3, Fig. 7). This observation indicates that both *Fordilla* and *Pojetaia* are suboval to slightly elongated and cannot be distinguished by this character alone. The occurrence of a posterior auricle (Plate 2, A–D) is hitherto rarely reported from *Fordilla*, but typical for *Pojetaia*. Nevertheless, faint remains of such an auricle are present in *F. sibirica* and *F. germanica*, too (Krasilova 1977, pl. 2, figs. 1, 3; Elicki 1994, Fig. 4.13; discussion above).

The specimens from Turkey are assigned to the genus *Fordilla* because of the anterior muscle scars, general outline, size, umbo characteristics, and the hinge construction. The auricle seems to be better developed than in other *Fordilla* (discussion above), and the Turkish specimens may represent a new species of this genus. Due to the imperfect preservation, however, especially of muscle scars on the steinkerns, open nomenclature is preferred here. *Fordilla* sp. from Turkey represents the first report of the genus from strata of the traditional “Middle Cambrian” age (first stage of the “third series” of the Cambrian).

Palaeoecological and palaeogeographical conclusions

Bivalvia from western Perigondwana were first reported from Germany (Elicki 1994) followed by discoveries in Morocco (Geyer and Streng 1998) and Turkey (herein). The few hundred remains hitherto found from this region are nearly exclusively represented by steinkerns of the genera *Pojetaia* and *Fordilla*.

The material from Germany (Plate 3) comes from limestones of the late “Early Cambrian” Upper Ludwigsdorf Mbr. of the Saxothuringian terrane (corresponding to the later Banian of the western Gondwana standard, to higher Marianian of Spain, and to the early upper stage of unnamed “series 2” of the ICS scale, respectively). At that time, this terrane was probably situated in a sub-equatorial position within a hot climate belt (Courjault-Radé et al. 1992; McKerrow et al. 1992; Álvaro et al. 2000, 2003), but alternative reconstructions assume higher southern latitudes (Meert and Liebermann 2004; Cocks and Torsvik 2006). Here, we follow the former model mainly because of distribution patterns of archaeocyaths and of warm water sediments. The bivalve-bearing sediments from Germany are bioclastic wackestones to floatstones containing phosphatic black pebbles. Sedimentary structures are wave ripples, cross bedding, load casts, and small channels, indicating a rather shallow environment. Associated fossils are mainly represented by echinoderms and cancelloriids, but trilobites, hyoliths, further mollusks, poriferans, and *small shelly fossils* (hyolithelminths, cambroclaves, *Rhombocorniculum*, *Halkieria*, etc.) occur, too (Elicki 2007). Lithological as well as palaeontological data indicate subtidal, open-marine conditions of a transgressive system. The sedimentation rate was probably low. Sporadically, the sediments may have been reworked by higher energy events (Elicki 1994). Following taphonomic features (no abrasion, rare broken fossils), the fauna is regarded as autochthonous to par-autochthonous (Elicki and Schneider 1992). The bivalve level is immediately below nodular limestones, which are seen as the start of the drowning of the environment. So, a quiet position on a muddy carbonate ramp with a

reduced sedimentation rate as a living place for the bivalves can be concluded. In contrast, no bivalves occur in oligotrophic ramp environments of the German “Early Cambrian.” Such habitats are characterized by calcimicrobial carpets and archaeocyathan mounds (Elicki and Debrenne 1993; Elicki 1999; Wotte 2004), and occur in slightly older deposits of a possibly different Perigondwanan shelf fragment about 100 km to the northwest (Leipzig area).

Bivalves from the Çal Tepe Fm. of Turkey come from different facies types of a transgressive succession. As stated above, few specimens were found in limestones of bioturbated peloidal facies (latest “Early Cambrian,” Black Limestone Mbr.) and of echinoderm wackestone to packstone and floatstone facies (early “Middle Cambrian,” Light Grey Limestone Mbr.). The vast majority of specimens were found in samples of a bioclastic wackestone, rich in disarticulated cancelloriids and echinoderms, accompanied by poriferids, mollusks, trilobites, brachiopods, and *small shelly fossils*. Although broken or abraded elements are missing, the fossil remains of this horizon are smaller and thinner than below, which can be interpreted as an indication for some moderate transportation within an open-marine environment (parautochthonous) to a slightly more distal area. As in the German deposits, nodular limestones occur in short distance above the sampled level, indicating a distinct increase of the sea level. Palaeogeographic models of this time show this part of Turkey in a latitudinal position similar to that of the Saxothuringian terrane, but probably some degrees closer to the palaeo-equator (Brock et al. 2000; Gozalo et al. 2007). Sedimentological characteristics and the recent findings of archaeocyathan constructions (Çal Tepe Fm. near Eğirdir and some meters below the bivalve levels in the type section near Seydişehir; Göngüoğlu pers. comm.; Elicki et al. 2007) support this assumption.

Moroccan bivalves, reported by Geyer and Streng (1998), belong to the early “Middle Cambrian” *Cephalopyge notabilis* biozone (Moroccan scale) and are approximately coeval to the Turkish specimens of the Light Grey Limestone Mbr. The fossiliferous horizon in Morocco represents a hash limestone (“Brèche à *Micmacca*” Mbr. of the lower Jbel Wawrmast Fm.) intercalated between and lying on top of LLH-type stromatolites (= laterally linked hemispheroids), typical for deposition in high-energy intertidal to shallow subtidal environments (Logan et al. 1964). Along with the allochthonous bivalves, reworked remains of trilobites, brachiopods, echinoderms, and various *small shelly fossils* occur. The depositional environment is interpreted as shallow-marine, high-energy nearshore to shoreface (Geyer and Landing 1995; Geyer and Streng 1998). Palaeogeographic models place Morocco south of Spain, possibly at around 40° S latitude (McKerrow et al. 1992; Courjault-Radé et al. 1992), but around 60° S

according to other reconstructions (Meert and Liebermann 2004; Cocks and Torsvik 2006).

Most authors interpret an infaunal mode of life for *Pojetaia* and *Fordilla*. This conclusion is mainly based on the laterally compressed shape and the articulated preservation, which is seemingly the most common case (e.g., Krasilova 1977; Runnegar and Bentley 1983; Jermak 1986, 1988; Runnegar 1990; Geyer and Streng 1998; Parkhaev 2001; Elicki and Gürsu herein). Nevertheless, Skovsted (2004) reported a *Pojetaia* collection from the “Early Cambrian” of Greenland represented by 90% single valves or internal molds compared to about 23% for Australian collections. Additionally, Kouchinsky (2001) speculated that disarticulated valves possibly could be present in the host sediments, but selective phosphatization combined with dilution during chemical preparation of the rock samples in the laboratory may lead to secondary preservation effects within the residues (only articulated and phosphatized specimens survived this procedure). Pojeta et al. (1973) in their investigation on *Fordilla troyensis* pointed to the very well-developed anterior end and related musculature in this species and used it as a further argument for an infaunal mode of life (the anterior musculature is commonly distinctly reduced in epifaunal bivalves). Runnegar and Bentley (1983) observed that *Pojetaia runnegari* from South Australia is not bored by endolithic algae, but accompanying fossils (e.g., monoplacophorans) are affected in that way, which these authors interpreted as additional evidence for the infaunal model. In contrast to the articulated Cambrian bivalves from Germany (Plate 3, G), the material from Turkey does not show any activity of endolithic algae.

In contrast, other authors have proposed a suspension feeding, epifaunal, crawling mode of life on firm bottoms (Tevesz and McCall 1976, 1985; Vogel and Gutmann 1980). They argue that articulated preservation does not depend on an infaunal habitat in any case. Especially in tiny modern epifaunal clams of only a few millimeters size, valves usually do not spring open after death. Moreover, the multiple-layered construction of the ligament area in *Pojetaia* may indicate that the ligament was rather weak, but for passive opening an elastic ligament would be needed. In epifaunal habitats a passive opening depends—beside on the ligament—mainly on the decay rate of the muscles and the occurrence of water currents (Tevesz and McCall 1985). The mentioned authors have investigated modern assemblages coming to the result that only up to 10% of infaunal clams of the upper 30 cm of the sedimentary column were finally embedded with closed valves. The reported lack of endolithic borings could also be interpreted by a host-specification of the parasites (mineralogy of the shell, specific living conditions, etc.). Tevesz and McCall (1985) further noted that posterior and anterior

adductor muscles of *Pojetaia* are of distinctly different size (the first is relatively large; the latter is highly reduced or absent, p. 1328), which contradicts an infaunal mode of life where such muscles are generally similarly sized. Additionally, the authors mentioned that modern burrowers show a rather continuous pallial line and not the typical interrupted pattern of pallial muscle scars developed in *Pojetaia*. It has to be noted, however, that in *Fordilla* a less interrupted line of muscles is present.

Thus, for Cambrian bivalves, the kind of relation to the substratum is hard to estimate. Many usual features helpful in larger sized and/or phylogenetic younger bivalves can seemingly not be adopted here. This problem extends to the speculation on the feeding strategy of the early bivalves, too. There is no report of a pallial sinus or of a siphon as in modern species. Runnegar and Bentley (1983) argued that *Pojetaia* probably was an “inhalant” deposit feeder using the ciliated body and mantle surface to collect food particles. In this case, the water was entering the body anteriorly and/or ventrally. Reid et al. (1992) reported minute modern bivalves of less than 3 mm in size that pick up food particles with the foot. If epifaunal, the Cambrian clams may have obtained food by suspension feeding from the water column.

Runnegar and Bentley (1983) suggest a lecithotrophic mode of early ontogenetic development for *Pojetaia runnegari* with a rather short planktic larval stage, because of their small size. Their comparison of growth patterns of *Pojetaia* with those of living nuculoids led to the assumption of a generation time of about 1 year or less. As the habitats were situated in low latitudes, these authors assume that an annual reproductive cycle is rather unlikely in this genus.

Summarizing the data from the published literature and from our own investigations in various regions of western Perigondwana, *Pojetaia* and *Fordilla* together represent nearly 100% of the reported Cambrian bivalves from this palaeogeographic region and occur in two different depositional facies realms: (1) in autochthonous to par-autochthonous, subtidal muds (e.g., in the Upper Ludwigsdorf Mbr., Germany, and in the lower Çal Tepe Fm., Turkey) and (2) in allochthonous, very shallow subtidal to intertidal hash layers (e.g., in the “Brèche à *Micmacca*” Mbr., Morocco). The first facies is suggested as the usual habitat where the sedimentation rate was reduced and deposition took place under rather quiet water conditions, which may have been disturbed only sporadically by high energy events (for Germany compare Elicki and Schneider 1992; Elicki 1994). This interpretation corresponds with that given by Runnegar and Bentley (1983) for the Australian specimens. So, a very proximal higher energy position of the habitats of both these genera is rather unlikely. Enrichments in very shallow and marginal deposits (second facies) are allochthonous.

Given the extremely wide palaeogeographic distribution of *Pojetaia* and *Fordilla*, it is rather surprising that they have not been found yet in the other western Perigondwanan regions (Spain, France, Sardinia). Generally, we agree with Geyer and Streng (1998) that the nearly global distribution of the genus *Pojetaia* (West and East Gondwana, Baltica, Laurentia, Siberia) suggests that the reported specimens may rather represent different species. This concept may be supported by limited migration abilities, which can be concluded when the assumption of Runnegar and Bentley (1983) of a lecithotrophic larval stage, which means a relatively short planktonic phase (Sommer 2005), is accepted. A lecithotrophic early ontogenetic stage is typical for primitive mollusks (Peterson 2005), especially for the small-sized Cambrian species (Chaffee and Lindberg 1986). This argumentation is valid for all “Early Cambrian” mollusks and led Gubanov et al. (2004) to the conclusion of a closer connection between Cambrian palaeocontinents. On the other hand, more closely connected habitats contradict the above-mentioned suggestion of geographically induced species separation. In this case, the very small differences in *Pojetaia* species, which are evaluated as taxonomically significant by Geyer and Streng (1998), may indeed rather fall in the range of intraspecific variability.

Nevertheless, it is evident that the distribution of the species of *Pojetaia* and *Fordilla* in western Perigondwana is not limited by geographic separation (e.g., separate basins). During recent years the connection and brisk faunal migration along the whole European shelf segment of Gondwana is indicated by various fossil groups (archaeocyaths, trilobites, *small shelly fossils*; e.g., Pillola 1991; Perejón 1994; Elicki and Debrenne 1993; Geyer and Elicki 1995; Sarmiento et al. 2001; Álvaro et al. 2003; Gubanov et al. 2004; Elicki 2006, 2007; Gozalo et al. 2007). Two reasons may explain the phenomenon of missing bivalves in large areas of western Perigondwana: (1) the state of knowledge regarding *small shelly fossils* from Spain and Sardinia is rather low (Fernández-Remolar 2001; Elicki and Pillola 2004; Wotte 2006) and (2) the investigation hitherto carried out has not been done in the critical sedimentary facies realm. As stated above, the bivalves seem to occur in not very shallow, subtidal deposits of transgressive successions, in limited windows shortly before the Perigondwanan platforms were rapidly drowned. Additionally, oligotrophic environments of archaeocyathan-calcimicrobial facies or regions with high carbonate precipitation rates, such as very shallow areas of platforms or ramps, were seemingly not preferred by bivalves (see above), but such environments are often the focus of palaeontological investigation in carbonates because of searching for biostratigraphically significant taxa (e.g., archaeocyaths). In Sardinia, for example, nearly

exclusively nodular limestones of the drowning stage were investigated for *small shelly fossils* (Elicki and Pillola 2004). But in Germany as in Turkey, bivalves occur in the short stage before this lithofacies, near the end of the ramp or platform stage, immediately at the opening of the environment and beginning of the drowning. There is no reason to assume that *Bivalvia* known from the southern as well as from the northern edge of Perigondwana's European shelf do not occur in palaeoecologically equivalent strata in between. Future investigations on the critical ecostratigraphic portions of the successions are needed to fill this gap.

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