Early ontogeny of Jurassic bakevelliids and their bearing on bivalve evolution

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Larval and earliest postlarval shells of Jurassic Bakevelliidae are described for the first time and some complementary data are given concerning larval shells of oysters and pinnids. Two new larval shell characters, a posterodorsal outlet and shell septum are described. The outlet is homologous to the posterodorsal notch of oysters and posterodorsal ridge of arcoids. It probably reflects the presence of the soft anatomical character post-anal tuft, which, among Pteriomorphia, was only known from oysters. A shell septum was so far only known from Cassianellidae, Lithiotidae, and the bakevelliid *Kobayashites*. A review of early ontogenetic shell characters strongly suggests a basal dichotomy within the Pteriomorphia separating taxa with opisthogyrate larval shells, such as most (or all?) Praecardioida, Pinnoida, Pterioida (Bakevelliidae, Cassianellidae, all living Pterioidea), and Ostreoida from all other groups. The Pinnidae appear to be closely related to the Pterioida, and the Bakevelliidae belong to the stem line of the Cassianellidae, Lithiotidae, Pterioidea, and Ostreoidea. The latter two superfamilies comprise a well constrained clade. These interpretations are consistent with recent phylogenetic hypotheses based on palaeontological and genetic (18S and 28S mtDNA) data. A more detailed phylogeny is hampered by the fact that many larval shell characters are rather ancient plesiomorphies.

Key words: Bivalvia, Pteriomorphia, Bakevelliidae, larval shell, ontogeny, phylogeny.

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Introduction

Jackson (1890) and Bernard (1898) were the first to comprehensively examine early ontogenetic shell stages of fossil and living bivalves. Thereafter, such studies were long neglegted, with some important exceptions, for example Kříž (1966, 1969, 1979, 1996); Dzik (1994), and Yancey and Heaney (2000) on lower to middle Palaeozoic praecardioids, cyrtodontids, and cardiolids, C.P. Palmer (1989) on Upper Jurassic oxytomids and oysters, Malchus (1995) on Upper Cretaceous and Eocene oysters, Knight and Morris (1996) on Lower Cretaceous inoceramids; LaBarbera (1974) on Miocene palaeotaxodonts and heterodonts, and Tanabe (1990) and Tanabe and Zushi (1988) on some Pliocene and Pleistocene arcoids. Cragg (1996) briefly reviewed the phylogenetic significance of some bivalve veliger characters. During the past six years I studied an exceptionally well preserved and diverse bivalve microfauna from a Middle Jurassic subsurface section from north-west Poland (Malchus 2000a, b, c, d, 2001; Malchus and Steuber 2002). This section yielded numerous larval and early postlarval shells of Bakevelliidae. These, together with additional material from Upper Jurassic outcrops in England and shells of extant species of other families from the western Mediterranean and the Red Sea, form the basis for the present contribution.

Early ontogenetic shell stages of Bakevelliidae were previously unknown. Thus, a rather detailed description is offered together with new aspects on extant pinnids and Jurassic oysters. In conjunction with earlier studies, the new data allow phylogenetic analysis of early ontogenetic shell characters across a wide stratigraphic and taxonomic range. This leads to a preliminary phylogeny hypothesis exclusively derived from early ontogenetic shell stages, and which can be compared to established hypotheses founded on independent palaeontological and genetic evidence. A complementary study on ligament ontogeny and evolution is being published elsewhere (Malchus in press).

Materials

Most of the studied specimens are from core sediments that were drilled from the Bajocian to Middle Callovian in north-west Poland. The core was drilled in 1937 near the small village of Kłęby (Klemmen), about 50 km north-east of Szczecin. In addition, a single specimen of Early Callovian age is described from a core near Karlshagen, about 30 km east of Greifswald, north-east Germany, about 80 km north-west of Kłęby. Another specimen, donated by C.P. Palmer (Natural History Museum, London) is from the *Aulacostephanus eudoxus* or *Aulacostephanus autissiodorensis* Zone of the Kimmeridge Clay (Upper Kimmeridge) which crops out at Osmington Mills, Dorset, south England. The remainder of the specimens were sampled from the *Aulacostephanoides*

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mutabilis Zone of the Kimmeridge Clay pit of the Blue Circle Cement Company near Westbury, Wiltshire, south England. Non-bakevelliid fossil material is from Kłęby and Westbury. For details on the stratigraphy see Malchus and Steuber (2002) and the literature cited therein.

Samples of Recent species are from the western Mediterranean (author's own material). Reference is also made to material from the Red Sea (see Rützen-Kositzkau 1999, for details), from which the Pterioidea and Ostreoidea were studied by myself. Some of the early ontogenetic pterioideans are described in Malchus (in press). The other specimens are currently unpublished.

All samples described in this study are housed in the Bundesanstalt für Geowissenschaften und Rohstoffe in Berlin (abbreviated BGR).

Methods

Microfauna including small bivalve specimens from the Kłęby and Karlshagen cores were already hand-picked from the little consolidated sediment by members of the Geological Survey of the former German Democratic Republic. Other Jurassic bivalves were obtained by wet-sieving the clay samples taken by myself. Samples from extant Mediterranean bivalves were caught in the plankton and by dredging in the bay of Banyuls (Golf de Lyon, north-east France) during various stays at the Laboratoire Arago, Banyuls.

Specimens were cleaned with water and alcohol, mounted on aluminium stubs and sputter-coated with gold-palladium for examination under a scanning electron microscope (SEM). Examination focussed on shell morphology, provinculum ontogeny, transition from larval to early postlarval hinge characters, and measurements of the length and height of the P1 and P2 stages, respectively. Incomplete specimens were only measured if breakage did not affect crucial reference points on the shell. Measured dimensions are defined in the following section.

The interpretation of the statistics follows results of Malchus (1999, 2000a, c, d, and unpublished) according to which the size of the P1 and the P2 (at metamorphosis) of bivalves is normally distributed. The 20 extant and seven fossil species thus far tested differ significantly at least by some of their dimensions of length, height and L/H ratio. The mean within-species variation of extant and fossil species was found to be lower than six percent (coefficient of variance,

CV), and this mean plus its 1.96 standard deviation (SD) remains below nine percent. Exceptionally high CV values generally result from inclusion of shells from immature larvae (prior to metamorphosis), mixture of stratigraphically distant populations (phylogenetic size changes), and/or insufficient sample size.

Sample sizes of about 25 individuals (measurements) per species are necessary for significance tests if the CV is about six percent, and over 50 measurements if the CV reaches nine percent (Malchus 1999: fig. 16). Sample sizes of the present analyses are considerably lower, and the interpretation of the CV values therefore should be considered as being orientative.

Terminology and definitions

The definitions of shell types and correlated modes of development given below should be understood as generalisations, which arguably cover the taxa discussed here. Some exceptions will be mentioned. However, there exist many intermediate forms the discussion of which is beyond the scope of the present paper. Especially the pre-metamorphic shells of entirely brooded species may be very distinct from purely planktotrophic or combined lecithotrophic-planktotrophic species (e.g., species of *Cratis*, *Chlamydella*, among many others; see Hayami and Kase 1993).

Ligament.—The first "ligament" of the larvae is the uncalcified periostracal junction between left and right valves, which, at least in oysters, becomes thicker during larval growth (Waller 1981). A fibrous resilium is present in the P2 of most bivalves (Waller 1998).

Generally speaking, the ligament of adult bivalves consists of an outer lamellar sublayer and an inner fibrous—or rarely granular in some Palaeotaxodonta—sublayer. The extremely thin periostracum covers the lamellar sublayer externally (for details refer to Carter 1990, 2001; Waller 1990). In all extant and fossil Pteriomorphia examined by myself, and according to Thomas R. Waller (personal communication 2001), in bivalves in general, the first adult fibrous resilium is a continuation of the larval fibrous ligament. However, in many Pteriomorphia it is abandoned shortly after metamorphosis (Malchus in press; this study).

Nepioconch.—The nepioconch (N) is the earliest post-metamorphic shell. In most cases, the shell mineralogy, composi-

Fig. 1. **A–D**, **F–G**. Morphotype 1, all specimens × 50. **A**. P2-RV, arrows indicate position of pd-outlet; BGR X10859-9. **B**. RV, earliest nepioconch, with initial layers of nacre, still P2 size, BGR X10843-7. **C**. LV, nepioconch with P2, BGR X10860-2; C_1, nepioconch with P2; C_2, ventral view with fibrous ligament pits (1 and 2) and anterior tooth. **D**. LV, nepioconch with P2, ventral view showing 2 ligament pits (1, 2) and anterior tooth socket (ts) and tooth, BGR X10862-3. **F**. RV nepioconch with P2, with 2 ligament pits preserved, BGR X10862-1. **G**. P2-RV of earliest nepioconch, BGR X10863-3. **E**, **H–M**. Morphotype 2. **E**. P2-RV, BGR X10854-6; E_1, magnification as for morphotype 1 for comparison, × 50; E_2, × 75. **H**. P2-RV, BGR X10854-7; H_1, arrow indicates position of pd-outlet, × 75; H_2, dorsal view with interlocking type of valve margin, arrows indicate position of pd-outlet, × 125. **I**. RV, early nepioconch, with well preserved P2, BGR X10862-4, × 60; I_2, ventral view, 2nd ligament pit largely broken, × 75. **K**. LV early nepioconch with P2, BGR X10863-10; × 75. **L**. RV early nepioconch, ventral view, with 3 ligament pits, anterior tooth and tooth socket (ts), outer prismatic shell layer below tooth socket (arrow) is much thicker than on rest of shell, BGR X10843-8, × 40. **M**. RV early nepioconch, BGR X10862-6; M_1, close up of outer prismatic layer of M_2, × 75; M_2, showing four ligament pits and anterior tooth and socket (ts), × 30.
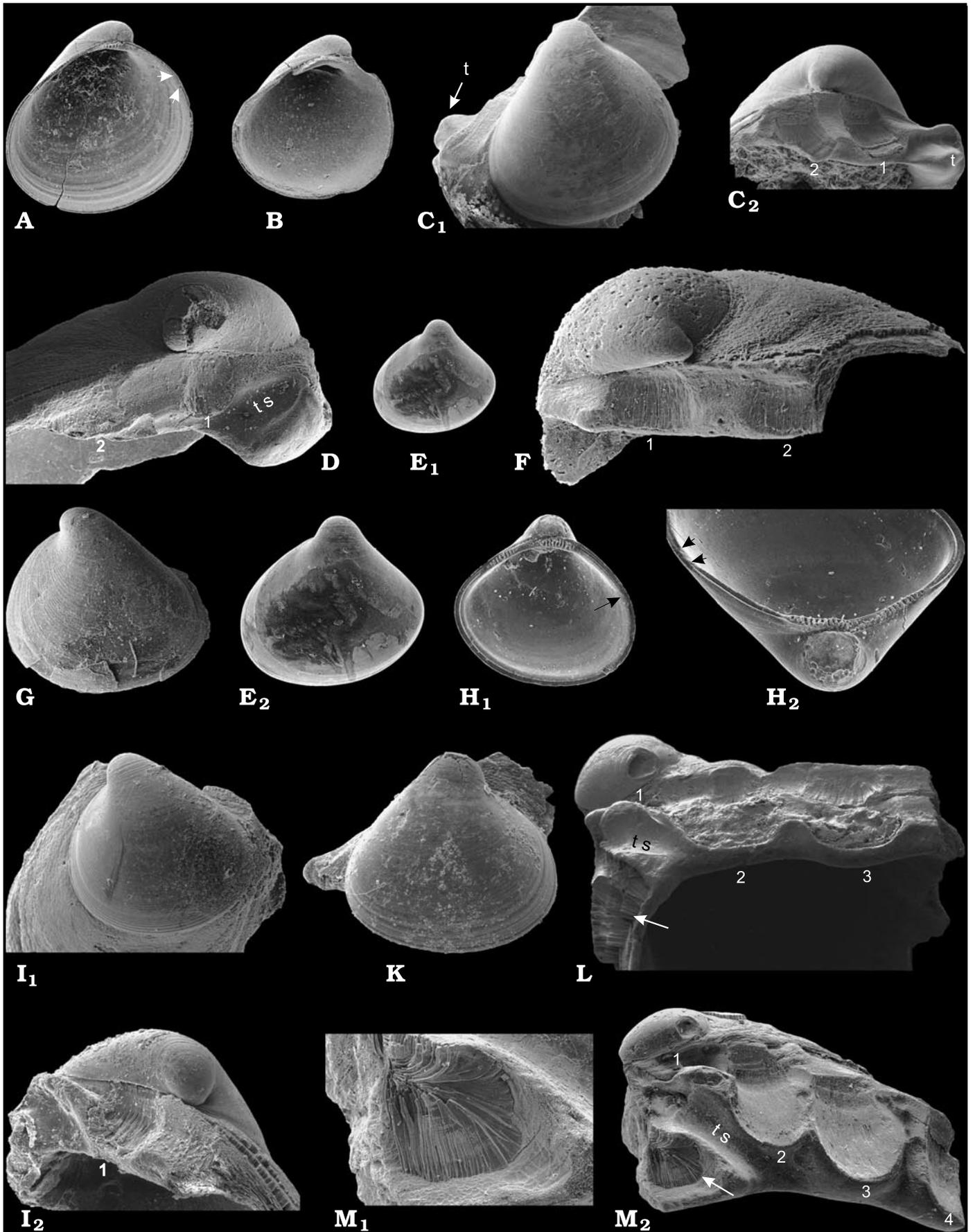
tion and microstructure change drastically after metamorphosis, so that the boundary between prodissoconch 2 and nepioconch is clearly visible (but see discussion on P2). For example, nacre forms exclusively post-metamorphically. In many bakevelliid specimens discussed here, nacre can be shown to form directly after metamorphosis covering the larval shell internally.

The nepioconch is often distinguishable from later shell stages on the basis of morphological, microstructural and/or sculptural differences. However, not all species show such differences.

Opisthogyrate umbo and related terms.—Shells with posteriorly coiled (= opisthogyrate) umbones indicate that the organism grew anteriorward along a more or less pronounced helical growth trajectory. The contrary is the case in prosogyrate shells. Ligament growth directions are naturally correlated with the growth trajectory of the animal or at least the mantle, because the ligament is formed by (specialised) mantle cells. Thus, ligament growth is oriented anteriorward (prosodetic) in opisthogyrate shells and posteriorward (opisthodetic) in prosogyrate shells. Note that helical growth may occur early or late in ontogeny and may change directions various times during ontogeny (for details see Malchus in press).

Prodissoconch 1.—The prodissoconch 1 (P1) is the first (generally) mineralized, aragonitic shell formed during the ontogeny of a bivalve. Larval shells of many palaeotaxodont bivalves and of *Planktomya* spp. (Montacutidae; see Gofas 2000) apparently remain largely uncalcified (Allen and Scheltema 1972; Zardus and Morse 1998: 237).

Entirely or partially planktotrophic species typically possess a superficially smooth P1 with respect to the P2 (but see Carriker and Palmer 1979, and Waller 1981 for ultrastructures). Subordinate, commarginal growth lines or increments commonly occur in later P1 stages (Ó Foighil et al. 1999: fig 2a; see also Carriker and Palmer 1979: fig. 2) but may be missing owing to environmental factors (Ó Foighil 1986).

Prodissoconch 2.—The prodissoconch 2 (P2; larval shell, veliger shell) is the second, pre-metamorphic, (generally) mineralized, aragonitic shell, typically produced by planktotrophic larvae with a longer free living veliger stage (of at least a couple of days). Characteristic features include (1) a narrow trough between P1 and P2; (2) prominent, commarginal growth lines (see Waller 1981, for more details); (3) relatively inflated or convex shell (at least one valve); and (4) often a larval fibrous ligament. Prominent hinge teeth are typical of the P2 of planktonic larvae but occur as well in taxa with purely lecithotrophic development such as the Philobryidae (Bernard 1897: figs. 4-1, 4-3, 4-4; personal observations). Sculptural elements other than commarginal ones are generally lacking in planktic planktotrophic taxa. But, fine antimarginal threads are known from *Crenella* (Crenellinae) (e.g., Hayami and Kase 1993: fig. 145; personald observations) and early post-metamorphic shells of the Dacrydiinae

and some Nuculidae (Gofas and Salas 1996; Salas and Gofas 1997).

Typically, purely planktotrophic species have a small P1 (roughly 35–100 mm) and a considerably larger P2 resulting in a low P1/P2 ratio (< 0.4). This ratio tends to be above 0.6 in species with a combined lecithotrophic-free living planktotrophic development. Purely lecithotrophic species have but a narrow shell fringe representing the P2 (e.g., Ockelmann 1965, 1983; Berkman et al. 1991).

Posterodorsal notch.—The term was coined by Waller (1981) to describe a small sinoidal recess of the posterodorsal shell margin of the left valve (LV) of oysters. It forms at or shortly after the beginning of the growth of the P2 shell and ends at the P2/nepioconch boundary (compare Fig. 6C). The notch leaves a conspicuous antimarginal growth track (fasciole, *sensu* Carriker and Palmer 1979) on the posterodorsal exterior of the left valve, which is morphologically reminiscent of the selenizone of some archaeogastropods. Notch and fasciole are typical of all LVs of living and fossil oysters with an unequivocal P2 phase. Right valves only show a minimal sinuosity of the shell margin (if at all) which causes a very faint, narrow concave growth track on the exterior of the P2.

The fasciole differs microstructurally from the remainder of the shell by a coarser granular prismatic outer shell layer (Malchus 1995: pl. 4: H, I, L). It is weakly convex and becomes slightly wider during growth. The sinuosity of the right valve is not microstructurally different from the rest of the shell. Both notch and sinuosity are lacking in species of *Tiostrea* owing to extraordinary long brooding (Jozefowicz and Ó Foighil 1998: 432; Malchus 2000b).

Posterodorsal outlet (new term).—Valve margins of the P2 of *O. edulis* L. fit into each other in a "tongue-in-groove fashion" (Waller 1981: 47). Waller observed that the internal commarginal ridge bounding the groove is interrupted at the site of the pd-notch (see also Carriker and Palmer 1979: figs. 39, 40; Malchus 1995: pl. 4: G, H). The new term "posterodorsal outlet" describes the complementary structure in the right valve of oysters (Malchus 1995: pl. 3: A; Fig. 6B, D) and, as will be shown, of many other Pteriomorphia.

Posterodorsal ridge.—The term has been recently created by Steffen Kiel (personal communication 2003) to describe a narrow, round-crested, posterodorsal ridge found in planktotrophic larval shells of various Jurassic to recent arcoid species. It is also present in Jurassic *Grammatodon* and recent *Striarca* studied by myself (unpublished). It occupies the same position as the ostreoidean fasciole. However, according to Steffen Kiel, the ridge is found on both valves, is thinner than the fasciole and does not widen during P2 growth. Although not studied in detail, it does apparently not differ microstructurally from the remainder of the shell (present observation).

Provinculum (amended definition).—The definition as given by Cox, Nuttal, and Trueman (1969: N107) reads: "Median part of hinge margin of prodissoconch, usually bearing small teeth
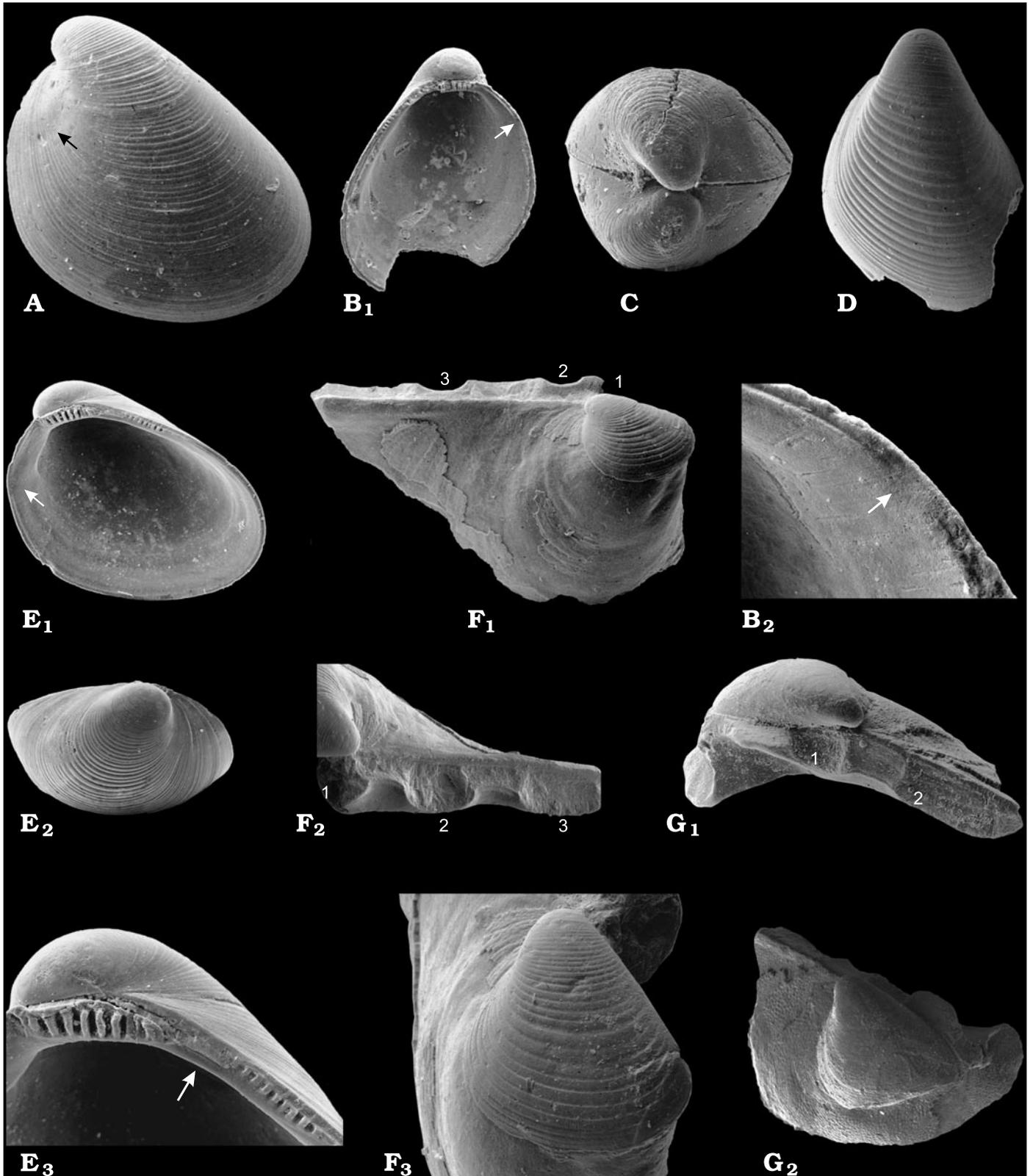
Fig. 2. Morphotype 3. **A**. P2-RV, arrow indicates slight shell deflection in postero-dorsal margin, which corresponds to growth track of pd-outlet, BGR X10864-3, × 100. **B, G**. P2-RV, BGR X10864-5. **B**. Arrow indicates position of pd-outlet, × 100. **G**. Close up of posterior-dorsal shell margin with outlet, × 500. **C**. P2, articulated shell, RV on top, dorsal view, note equivalve condition, BGR X10861-3, × 100. **D**. P2-RV, BGR X10861-8, × 100. **E**. P2-LV, BGR X10849-8; E_1, arrow indicates growth track and position of pd-outlet, × 100; E_2, dorsal view, × 100; E_3, close up of hinge area, arrow indicates leading edge of ligament, × 250. **F**. LV nepioconch with P2, BGR X10860-1. F_1, dorsal view, position of ligament pits indicated (1-3), × 40; F_2, ventral view of ligament area, 1st ligament pit broken, × 40; F_3, close up of P2, × 100. **G**. RV nepioconch with P2, BGR X10862-2. G_1, ventral view, × 40; G_2, dorsal view onto P2, × 40.

or crenulations." This definition is incomplete compared to the definition of "hinge" for adult bivalves (p. N105): "Collective term for structures of dorsal region, which function during opening and closing of valves". Also, larval hinge teeth are not always restricted to the median part of the larval hinge, especially in fossil Pteriomorphia. Thus, the term "provinculum" is extended to include the entire larval hinge system.

Shell dimensions.—The length of the prodissoconch is the widest distance between anterior and posterior shell margin parallel to the hinge axis of the D-shaped shell (P1) or parallel to the axis through the posterior row of hinge teeth of the P2 (valid only for strongly opisthogyrate taxa such as oysters and bakevelliids). Correspondingly, the prodissoconch height is the widest distance between the dorsal and ventral shell border and vertical to the above mentioned axes.

Review of phylogenetic hypotheses

According to Carter (1990), the Bakevelliidae most likely evolved from Permian Pterineidae which have a fossil record from the lower Middle Orovician to the Upper Permian. This view is consistent with the most recent review of the Bakevelliidae (Muster 1995), but it now appears that the Bakevelliidae originated in the Carboniferous (Thomas E. Yancey, personal communication 2001).

The calcitic prismatic-nacreous shell of adult bakevelliids, their shell morphology and/or the presence of a posteriorly extending, multivincular ligament as well as similar palaeobiogeographic distributions suggest a close relationship, if not ancestry, to the Triassic Cassianellidae, Lower Jurassic Lithiotidae, Triassic to living Pteriidae, the enigmatic Triassic Dattidae, Isognomonidae, and the Jurassic Retroceramidae (Ichikawa 1958; Jackson 1890; Chinzei 1982; Crampton 1988; Seilacher 1984; see Carter 1990: 206ff, for an overview). In addition, recent genetic studies indicate a common root for living Pterioidea, Ostreoidea, and Pinnoidea (Campbell 2000; Hammer 2001; Steiner and Hammer 2000; Giribet and Wheeler 2002), which would place the Bakevelliidae at least on the stem line of modern Pterioidea and Ostreoidea, and suggests a close relationship with the Pinnoida. This latter view is supported by new microstructural and ligamental evidence that the Pinnoidea evolved from duplivincular Pterineidae (Pterioida) (Carter in press) (compare bakevelliid ancestor, above, and Table 1).

Table 1. Classification scheme integrating pteriomorphian taxa discussed in the text (mainly after Carter 1990, and Carter et al. 2000). The order of order-rank names is modified to unite taxa with opisthogyrate larval shells or anteriorward growing ligament (indicated by an asterisc * and (*), respectively). Note that Carter et al. (2000) did not analyze all higher-rank taxa of Carter (1990). For this reason and because Linnean rank names (order, superfamily, etc.) lose their hierarchical meaning in cladistics, the hierarchical positioning of the non-cladistically analyzed taxa must remain somewhat ambiguous. These taxa are shown in square brackets.

Subclass Palaeotaxodonta
    Superorder Nuculaniformii
    Superorder Nuculiformii
        Order Nuculoida
          • Nuculoidea: Nuculidae (*Nucula*, *Acila*), …
        Order Solemyoida
          • Solemyoidea: Solemyidae (*Solemya*), …

Subclass Autolamellibranchiata
    Superorder Anomalodesmata
        Order Modiomorphoida
    Superorder Pteriomorphia
        Family Evyanidae
        Family Colpomyidae
        Order Mytiloida
          • Mytiloidea: Mytilidae: Mytilinae (*Mytilus*), Musculinae (*Musculus*), Crenellinae (*Crenella*), Dacrydiinae, …
        Order Arcoida
          • [Cardioloidea: Cardiolidae, Slavidae
          • Arcoidea: Parallelodontidae (*Grammatodon*), Noetiidae (*Striarca*)
          • Limopsoidea: Limopsidae (*Limopsis*)]
        Order Cyrtodontoida
          • Cyrtodontoidea: Cyrtodontidae (cyrtodontids unspecified, …
        Order Pectinoida
          • [Monotoidea: Oxytomidae (*Oxytoma*, *Meleagrinella*), …]
    [Order Praecardioida*
          • Praecardioidea: Praecardiidae, Antipleuridae*, Praeostreidae*, Butovicellidae*, Lunulacardiidae* (after Yancey and Heaney 2000)
          • Inoceramoidea: Inoceramidae*, … (after Johnston and Collom 1998]]
    Superfamily Ambonychioidea*
          • [Inoceramidae*, …]
    Order Pterioida*
          • Pterioidea
          • Pterineidae
          • [Bakevelliidae*, Cassianellidae*, Lithiotidae, Pteriidae*, Dattidae, Isognomonidae*, Retroceramidae, Pulvinitidae(*), Malleidae*,...]
          • [Pinnoidea (?*Atrina*(*))]
    Order Ostreoida*
          • [?*Lopha–Enantiostreon*-stock
          • Ostreoidea*
          • Gryphaeoidea*
          • ?Chondrodontidae stock]

Fig. 3. **A–C.** Morphotype 4. **A.** RV, earliest nepioconch stage, BGR X10856-9; A_1, incipient nacreous shell layers, arrow points at rather straight posterior-ventral shell margin, × 60; A_2, close up of hinge, arrow points at post-larval fibrous ligament, which is detached from the still preserved row of larval denticles, × 200. **B.** P2-LV, BGR X10849-6; B_1, dorsal, close up view of umbo, arrow indicates approximate position of pd-outlet, which is not accompanied by a notch as in oysters (compare Fig. $6C_2$), × 250; B_2, internal view, arrow indicates position of pd-outlet, × 100. **C.** P2-LV, BGR X10855-5, × 100. **D–H.** Morphotype 5. **D.** P2-LV, BGR X10855-4, × 100. **E.** P2-RV, BGR X10855-3, × 100. **F.** BGR X10838-5; F_1, P2-LV, arrow indicates pd-outlet, × 100; F_2: close up of pd-outlet, × 700. **G.** Close up of pd-outlet (white arrows) and incipient secondary denticles (black arrow) of a P2-RV, BGR X10856-5, × 700. **H.** P2-RV, BGR X10856-4; H_1, entire valve, long arrow indicates position of pd-outlet, short arrow region of marked secondary denticles; H_2, close up of shell margin with secondary denticles, × 700. **I.** Morphotype 6, P2-LV, BGR X10846-1, × 100.
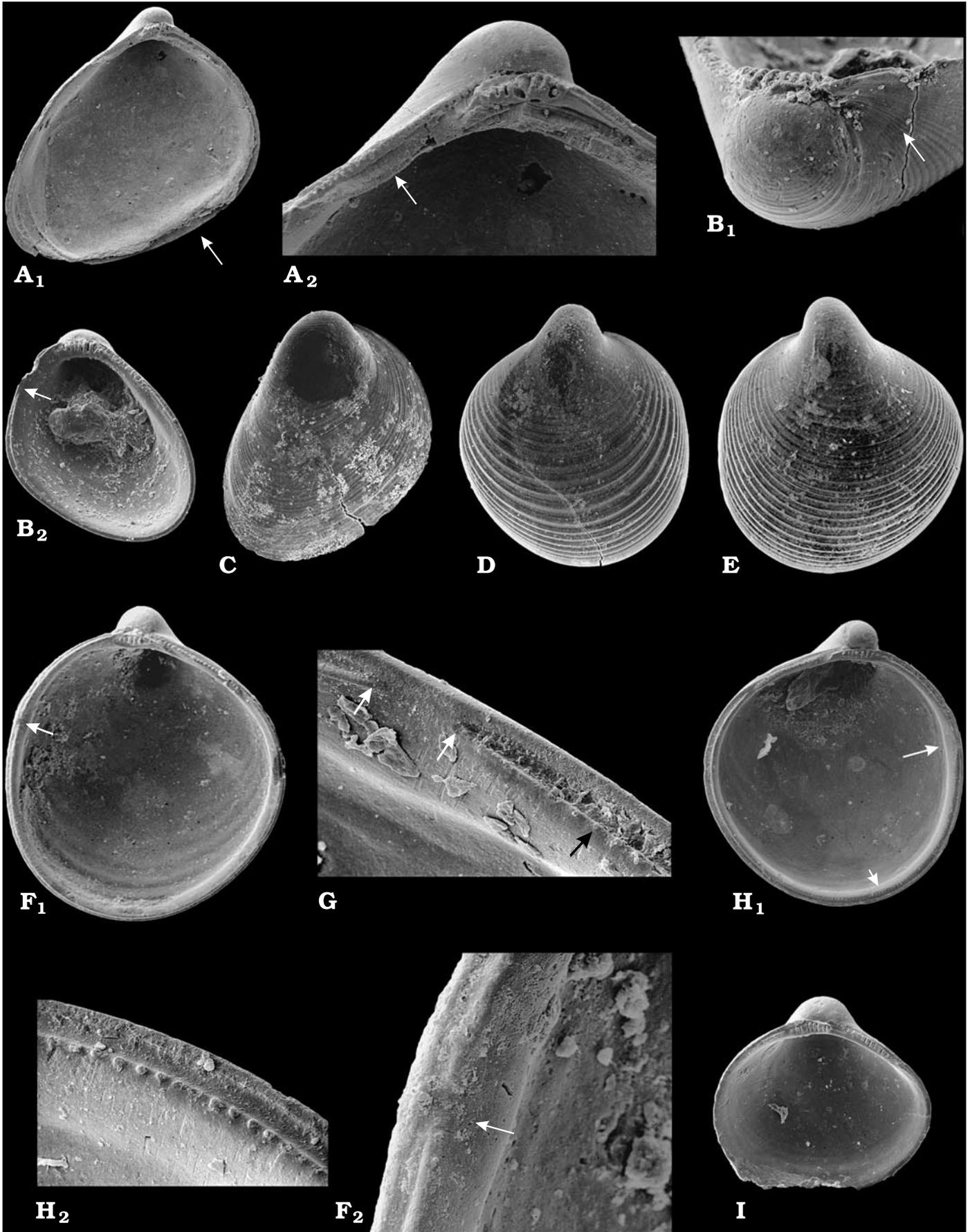
One of the few taxa that have not yet been linked to the Bakevelliidae are the Inoceramidae. According to Carter (1990: 199), this family belongs to the Ambonychioidea rather than Pterioida. Johnston and Collom (1998) placed the Inoceramidae in their amended order Praecardioida which, together with the Solemyoida constitute their subclass Cryptodonta (compare with Table 1). However, most recent phylogenetic analyses suggest that the Solemyoidea are the sister taxon of the Nuculoidea (Waller 1998: node PR2 and fig. 3; Giribet and Wheeler 2002: fig. 7) or that they evolved from nuculoid ancestors (Carter et al. 2000; Carter 2001), and hence should be included in the subclass Palaeotaxodonta. In addition, the Praecardioida *sensu* Johnston and Collom (1998) probably incorrectly contain the Cardiolidae, which is based on doubtful homologies of hinge characters between this family and the Inoceramidae (personal observations). The Cardiolidae are more likely related to the Arcoida (see Carter 1990: 181). However, this does not preclude the possibility that the Inoceramidae belong to the Praecardioida (see phylogenetic implications, below).

Descriptions

Previous ignorance concerning larval shells of bakevelliids and the lack of determinable adult shells in the present study hamper present generic and specific identifications. The fauna is therefore only tentatively classified into nine morphotypes, which arguably represent more than nine species.

Bakevelliidae (morphotypes 1 to 8)

Morphotypes 1 to 8 are characterized by a strongly opisthogyrate and large P2 between 400 and 845 μm in height, and a well-developed fibrous ligament (resilium) before metamorphosis. Their larval ligament grows anteriorward (except for M8) and divides the provinculum teeth asymmetrically into two series (compare Fig. 2E$_3$). The posterior series is situated below the larval beak and almost parallel to the straight hinge of the P1. The anterior series emerges from a point beneath the straight hinge of the P1 and above the ligament gutter and posterior teeth. It grows submarginally along the straight anterodorsal shell margin and at an angle to the posterior series. Right and left valves fit into each other in tongue-in-groove fashion, and both valves show a pd-outlet (Figs. 1H$_2$, 2B, 3B, F–H, 4A–D, F$_3$). There may be a weak sulcus developed on the exterior on the shell (Fig. 2A). However, a notch and fasciole are lacking (e.g., Fig. 3B$_1$).

The shell microstructure of the P1 was not examined specifically. The P2 is basically granular to granular prismatic and at least two-layered. Its thickness varies between 10 and 23 μm.

About half of the specimens of morphotypes 1 to 4 show at least some layers of post-metamorphic, nacreous shell. Larger nepioconchs are prismatic-nacreous and develop multiple resilifers containing disjunct fibrous resilia (Figs.

1C, D, F, L, M, 2F$_2$, G$_1$). Traces of lamellar ligament are missing probably owing to diagenesis. The first postlarval ligament is a ventralward growing continuation of the larval fibrous ligament, and is thus always found anterior to the beak (e.g., Fig. 1C$_2$–D, F, I$_2$, M$_2$). All following resilifers develop posterior to the beak and successively along a straight posterodorsal shell margin. The ligament area is nacreous; there is no indication of the outer prismatic shell layers invading the hinge area. Some nepionic specimens show initial stages of adult hinge dentition (Fig. 1C, D, L, M$_2$).

Morphotype 1.—This type is broad triangular with P1-lengths between 88 and 100 μm, P2-lengths between 628 and 745 μm (mean), and a length/height-ratio of the P2 between 0.91 and 1.08 (mean). The sculpture consists of comparatively weak and dense commarginal growth ridges (Fig. 1A–D, F, G).

Some nepioconchs show a short anterior tooth and/or socket. However, in all specimens from Kłęby the tooth or socket occur below the first adult ligament groove, whereas it is situated anterior to it in the specimen from Karlshagen (BGR X10860-2) (compare Fig. 1C and D). These two subtypes probably represent distinct species, which is not reflected by the coefficient of variance (CV) because of insufficient sample size (Table 2, M1).

Morphotype 1 occurs throughout the Upper Bathonian–Middle Callovian at Kłęby; specimen BGR X10860-2 is from the (?Lower) Callovian at Karlshagen.

Morphotype 2.—Morphotype 2 is very similar to morphotype 1 with respect to shell outline and sculpture (Fig. 1E, H–M). The P1-length ranges from 80 to 90.2 μm and those of the P2-lengths from 457 to 605 μm. Both P1 and P2 are thus smaller than in M1. That M1 and M2 do not represent a single species is also suggested by the relatively high CV values (Table 2, M1+2). This is even true for the CV of M2 alone. Concordantly, some specimens (Fig. 1E, H) show a slighly lower coiling intensity than others (Fig. 1G, I$_1$, K), which may indicate species differences.

Both subtypes co-occur with morphotype 1 in the Upper Bathonian–Middle Callovian at Kłęby.

Morphotype 3.—This type is characterized by a slender-triangular shape (Fig. 2A–G). The dorsoanterior shell flank slopes steeply; the posteroventral border is curved (in contrast to morphotype 4). The P1-length varies between 60 μm and almost 80 μm, with the exception of specimen BGR X10860-1 (Fig. 2F) from Osmington Mills (England) which reaches 95 μm. The P2 length ranges between 297 and 765 μm (including immature specimens), and the length/height ratio is generally below 1 (that is, length < height), except for two large specimens.

The extreme size range in P2-length reflects the inclusion of not full grown individuals. But, even considering only full grown larval shells (Table 3: M3a-P) or, in addition, excluding the smallest juvenile from Kłęby and the English specimen (Table 3: M3b-P) yields high CV values. This indicates that morphotype 3 encompasses more than one species,

Table 2. Statistics of the dimensions of morphotypes 1 and 2. Note that only those larval shells can be safely considered as full grown which show some post-metamorphic shell material. Abbreviations: CV, coefficient of variance; L, larval shell, M1, M2, M3, …, morphotype 1, 2, 3 …, N, number of specimens measured, P, postlarval shell (of which larval shell was measured), SD, standard deviation. Dimensions (mean, minimum, and maximum) are given in microns.

Morph	Stage	Variable	N	Mean	Min	Max	SD	CV
M1+2	L+P	Length	24	623	457	762	104.9	**16.8**
	L+P	Height	25	625	407	807	118.5	18.9
	L+P	Ratio	22	1.03	0.91	1.12	0.06	5.3
	P	Length	18	665	503	762	83.0	**12.5**
	P	Height	20	667	512	807	87.6	13.1
	P	Ratio	17	1.01	0.91	1.09	0.05	4.8
M1	L+P	Length	13	708	625	762	43.7	**6.2**
	L+P	Height	15	705	575	807	62.3	8.8
	L+P	Ratio	13	1.02	0.91	1.09	0.05	4.7
	P	Length	12	706	625	762	44.5	**6.3**
	P	Height	14	702	575	807	63.7	9.1
	P	Ratio	12	1.02	0.91	1.09	0.05	4.8
M2	L+P	Length	11	523	457	605	50.4	**9.6**
	L+P	Height	10	505	407	620	70.5	13.9
	L+P	Ratio	9	1.04	0.92	1.12	0.07	6.25
	P	Length	5	553	503	605	44.1	**8**
	P	Height	5	555	512	620	42.9	7.7
	P	Ratio	4	0.91	0.92	1.03	0.05	4.9

which is also indicated by morphological differences. Subtypes or different species may be represented by Figs. 2A, E, 2D, F, and 2G.

In addition, the first subtype (Fig. 2A) shows a tendency to become broad triangular near the end of the larval phase and is then difficult to distinguish from M1 and M2 (compare Fig. 2A, E_1, E_2 with Fig. 1A, C_1). Nevertheless, the sculpture tends to be coarser and the shell size of the P1 and/or P2 and/or the ratios are distinct (see Tables 2, 3).

Morphotype 3 is present in Upper Bathonian and Middle Callovian horizons at Kłęby and in the Kimmeridgian (Fig. 2F) from Osmington Mills (England).

Morphotype 4.—This type is very similar to morphotype 3. However, the posteroventral shell border is straight, not curved (Fig. 3A–C). Specimen BGR X10856-9 (Fig. $3A_1$) is internally covered by post-metamorphic nacreous shell layers. The size ranges and length/height ratios fall within those of morphotype 3, although the largest specimen reaches 845 µm in length. The CV of 40 percent of morphotype 4 reflects the inclusion of immature larval shells as well as small sample size (Table 3: M4-L+P, and M4-P). It may represent a pinnoidean rather than a bakevelliid species (see below).

This type is rare in the Upper Bathonian to Middle Callovian at Kłęby and in the Kimmeridge Clay at Westbury.

Morphotype 5.—This type is clearly distinct from all previous morphotypes owing to its oval (l < h) and more symmetrical shape, although the anterior shell border is more pointed than the posterior one (Fig. 3D–H). The P1 length is between 63 and 81 µm and the P2 length between 438 and 537 µm; the length/height ratio of the P2 is very constant between 0.86 and 0.89 (Table 3). A striking feature, only shared by morphotype 7, is the presence of small, bump-like to rectangular tubercles on the inner shell margin (ridge of the interlocking margins) anteroventral of the pd-outlet. The CV for morphotype 5 indicates that the sample represents a single species (Table 3). Postlarval shells are presently unknown.

This morphotype appears to be more common in the Upper Bathonian than the Middle Callovian at Kłęby.

Morphotype 6.—The shape of this type is oval in length (l > h) with a distinctly narrowly rounded anterior shell margin (Figs. 3I, 4A, B). Only three specimens were found. The P1 length ranges between 78 and 93 µm, the P2-length is 422 µm and 471 µm, respectively, and the P1/P2 ratio of one of the specimens is above 1. The number of specimens measured renders the CV uninformative (Table 3). Postlarval shells are presently unknown.

Two specimens come from the same horizon in the Middle Callovian at Kłęby. The third specimen is from the Kimmeridge Clay at Westbury.

Morphotype 7.—This type is almost round in outline, but with the anterior margin somewhat more narrowly rounded (Fig. 4C, D). One of the two specimens found shows the same type of tubercular shell margin denticles as M5 (Fig. 4D). The P1 length is 60 µm and 77 µm, respectively, the P2 length 521 and 522 µm, and the ratio is between 0.96 and 0.98. The CV is uninformative (Table 3). Postlarval shells are presently unknown. This morphotype is restricted to two horizons of the Middle Callovian at Kłęby.

Morphotype 8 (*Kobayashites*?).—Only two specimens were found of this type (Fig. 4E, F). It is oval in height and characterized by a short, internal shell septum, which sepa-

Table 3. Statistics of the dimensions of morphotypes 3 to 9. Note that only those larval shells can be safely considered as full grown which show some post-metamorphic shell material. M3b-P excludes one outlier and a specimen from England with respect to M3a-P. See descriptions for details. Abbreviations: CV, coefficient of variance; L, larval shell, M1, M2, M3, …, morphotype 1, 2, 3 …, N, number of specimens measured, P, postlarval shell (of which larval shell was measured), SD, standard deviation. Dimensions are given in microns.

Morph	Stage	Variable	N	Mean	Min	Max	SD	CV
M3a	L+P	Length	27	488	297	765	116.5	**23.9**
	L+P	Height	25	540	342	755	107.5	19.9
	L+P	Ratio	25	0.88	0.74	1.01	0.07	8.3
	P	Length	10	567	311	765	117.8	**20.8**
	P	Height	8	606	384	755	118.1	19.5
	P	Ratio	8	0.91	0.76	1.01	0.09	9.3
M3b	P	Length	8	609	528	765	74.8	**12.3**
	P	Height	6	656	549	755	73.2	11.2
	P	Ratio	6	0.92	0.76	1.01	0.09	9.7
M4	L+P	Length	6	519	288	845	208.3	**40.2**
	L+P	Height	7	546	347	860	173.3	31.8
	L+P	Ratio	6	0.91	0.83	1.04	0.09	9.5
	P	Length	2	753	661	845	130.1	**17.3**
	P	Height	2	747	633	860	160.5	21.5
	P	Ratio	2	1.01	0.98	1.04	0.04	4.4
M5	L	Length	8	502	438	537	38.2	**7.6**
	L	Height	8	573	510	618	42.2	7.4
	L	Ratio	8	0.88	0.86	0.89	0.01	1.3
M6	L	Length	3	433	407	471	33.5	**7.7**
	L	Height	1	394	394	394	–	–
	L	Ratio	1	1.07	1.07	1.07	–	–
M7	L	Length	2	521	521	522	0.7	**0.2**
	L	Height	3	537	533	543	5.3	0.9
	L	Ratio	2	0.99	0.96	0.98	0.01	1.2
M8	L	Length	2	412	377	447	49.5	**12**
	L	Height	1	532	532	532	–	–
	L	Ratio	1	0.84	0.84	0.84	–	–
M9	L	Length	10	298	284	321	11.1	**3.7**
	L	Height	8	296	288	315	9.2	3.1
	L	Ratio	8	1.00	0.99	1.02	0.01	1.2

rates the most dorsal shell cavity into two unequal parts (Fig. $4E_1$). The septum is fused with the posterior part of the provinculum and the bottom of the shell; it runs somewhat obliquely posterodorsal to anteroventral. The morphotype lacks the pronounced opisthogyrate umbo of the previous types, and a fibrous larval ligament is missing or has not yet appeared. Nevertheless, it possesses a tongue-in-groove shell margin, a pd-outlet (Fig. $4F_2$, F_3), and a general tooth arrangement as the other bakevelliids (Fig. $4E_3$, F_1). The P2 sculpture consists of relatively coarse growth welts. Postlarval shells are presently unknown.

The P1 measures 87 × 62 μm and 102 × 73 μm, respectively (length × height), which may indicate that the two specimens belong to different species. The P2 measures 381 × 437 μm and 447 × 587 μm, respectively. And the length/height ratios (P2) are 0.76 and 0.87. The CV is uninformative (Table 3). Both specimens are from the same horizon of the Middle Callovian at Kłęby.

Non-bakevelliid taxon

Morphotype 9.—This type is almost perfectly round, even though the posterodorsal shell margin is very faintly flattened in some specimens (Fig. 5A–E). Articulated shells are almost globular (Fig. 5D). The provinculum is nearly symmetrically divided by a central gap, which still (?) lacks a fibrous ligament (Fig. $5A_1$, C_1). The valves close in tongue-in-groove fashion and possess a pd-outlet (Fig. $5A_1$, A_2, C_1, E_1).

The interior shell margins carry a denticular structure reminiscent of teeth of a gear wheel. The denticles of the

Fig. 4. **A**, **B**. Morphotype 6. **A**. P2-LV, BGR X10866-9; A_1, entire LV, arrow indicates position of pd-outlet, × 100, A_2, close up of dorsal-central and posterior valve, × 250. **B**. P2-LV, external view, BGR X10846-2, × 100. **C**, **D**. Morphotype 7. **C**. P2-LV, BGR X10843-6; C_1, with pd-outlet indicated by arrows, × 100; C_2, close up, × 150. **D**. P2-RV, BGR X10856-6. D_1, close up of D_2, arrows indicate pd-outlet and below, incipient secondary denticles, × 150; D_2, internal view of entire valve, × 100. **E**, **F**. Morphotype 8. **E**. P2-RV, BGR X10859-7; E_1, close up of dorsal part of valve showing orientation of septum, × 250; E_2, entire valve, × 100; E_3, close up of hinge, arrow indicates assumed position of future resilium, note that the central provincular teeth of the anterior (left) row are broken, × 250. **F**. P2-RV, BGR X10859-6; F_1, close up of hinge area, arrow indicates assumed position of future resilium, × 250; F_2, entire valve, arrow indicates pd-outlet, × 100; F_3, close up of posterior shell margin with pd-outlet, × 500.
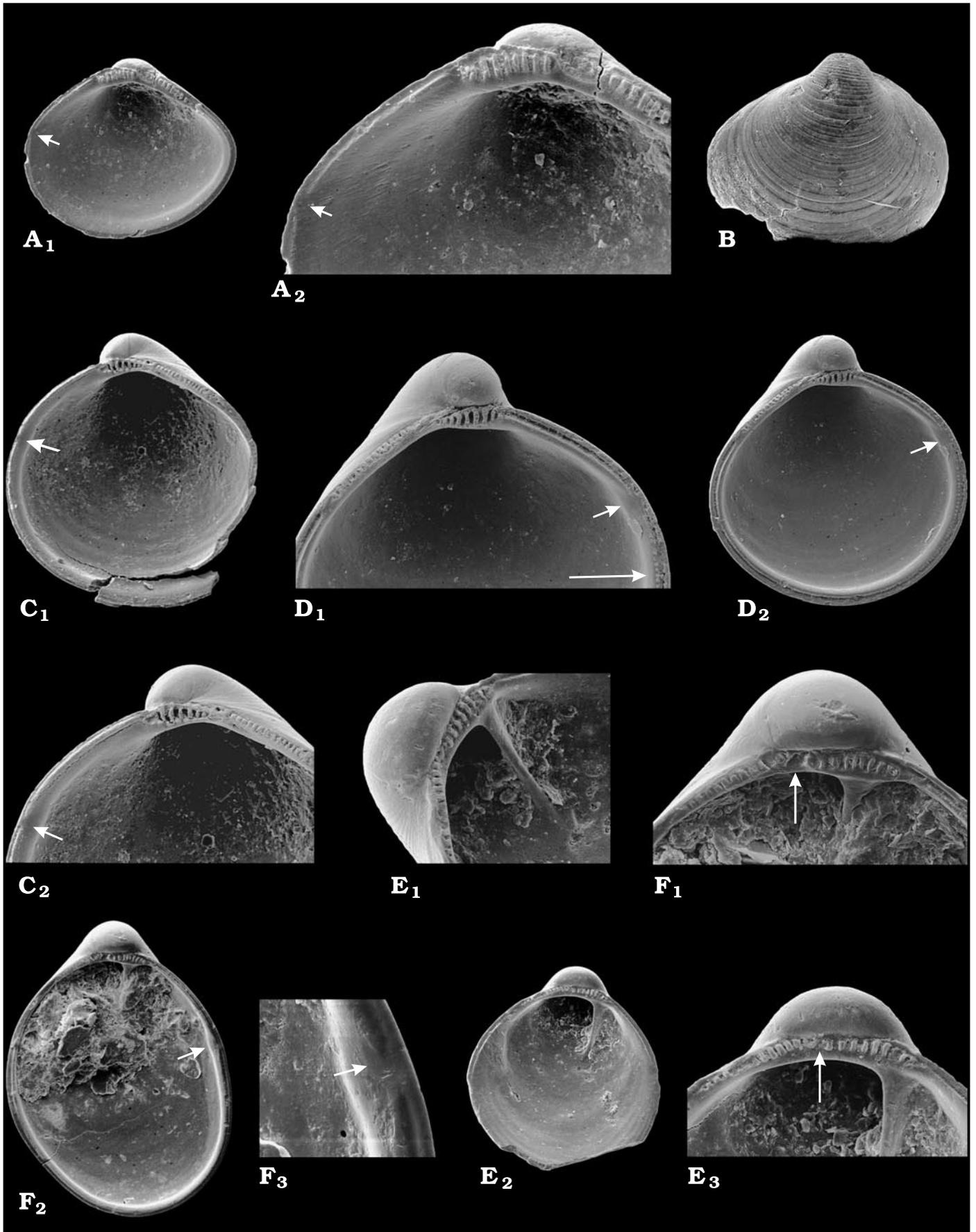
right valve are shaped like gothic window frames with their long axis oriented perpendicular to the shell margin (Fig. 5C$_2$). Correspondingly, the left valve possesses two sets of denticles. The outer set consists of short triangular denticles, which fit into the wedges between the pointed arches of two adjacent "windows". The denticles of the interior set are elongated rectangular and represent the "window" fillings (Fig. 5A$_3$). The shell has a sculpture of coarse growth welts.

The mean length of the P1 is 65 µm and that of the P2 is 300 µm; the L/H-ratio is 1. The CV of morphotype 9 indicates that the sample represents a single species (Table 3). Postlarval shells are presently unknown.

This type is found in large numbers in some horizons within the *Aulacostephanoides mutabilis* Zone of the Kimmeridge Clay at Westbury.

Comparisons

Morphotypes 1 to 8 share many shell characters with several pteriomorphian families, as noted below. Only morphotype 9 does not compare with any presently known larval shell type.

Inoceramidae.—Larval shells of Lower Cretaceous *Birostrina* and *Inoceramus* described by Knight and Morris (1996: text-fig. 2B) are extremely similar to morphotypes 1 to 7, including shape, sculpture and hinge details. With the help of recent observations on oysters and bakevelliids (Malchus 2000b, and this study), the original interpretation (cited below) of the hinge characters can be amended in some important details: "In our specimens, only the anterior hinge dentition is preserved, and then only in poor condition. The larval shells have numerous rectangular, 'taxodont'-like provincular teeth with rounded apices that are equal in size (text-fig. 4A, B). They are evenly projecting and regularly arranged on a raised ridge parallel to the anterio-dorsal margin. They are separated from the dorsal margin by a narrow groove (text-fig. 4B). Distal to the provincular teeth and within the groove, close to the anterio-dorsal margin, there is a series of at least ten very much smaller teeth (text-fig. 4C). The position of the ligament attachment cannot be ascertained from the specimens studied."(Knight and Morris 1996: 1033). Comparison of this description with that for morphotypes 1 to 8 given above strongly suggests that it is the posterior rather than the anterior part of the larval dentition, which sits on a raised ridge. The separated anterior series of smaller teeth most likely represents part of the anterior arm of the provinculum dentition as seen in all bakevelliids (Figs. 2E$_1$, 3I, 4A$_2$). Interpreted this way, the narrow groove dorsal of the ridge is most probably the larval ligament gutter (compare with Fig. 2E$_3$).

The prodissoconch sizes of these inoceramids are about 40 µm (P1), which is 50–100 percent smaller than in morphotypes 1 to 8. And the P2 is between 750 to 1000 µm long, which figures in the upper range and above the maximum sizes of the present samples. In addition, the ligament area of adult Inoceramidae is overgrown by a hypertrophied extension of the prismatic outer shell layer ("ligamentat", Johnston and Collom 1998) that was not observed here. And the resilifers do not indent the leading edge (ventral margin) of the ligament area (Johnston and Collom 1998), whereas this is the case in all specimens with postlarval hinges described in this study.

Isognomonidae.—The few prodissoconchs known from living species of the Isognomonidae differ by their tendency for much less pronounced opisthogyrate coiling. The larval ligament does not grow anteriorly beyond the larval umbo. From this point, the first postlarval resilifer emerges, which has a triangular shape. Figures in Jackson (1890: 329, fig. 30) and Bernard (1898: pl. 9: 5–8), as well as present observations on *Isognomon alatus* (Gmelin) from the Florida Keys suggest that all following resilifers are initially triangular and, importantly, oriented posteriorward before becoming rectangular and extending ventrally (Malchus in press). In contrast, the resilifers of the examined morphotypes extend anteriorly far beyond the larval umbo. And the first, adult fibrous ligament emerges from the whole ventral margin of the larval ligament. Thus, the first and all following adult resilifers are rectangular from the beginning (Figs. 1C$_2$, F, I$_2$, L, M$_2$, 2F$_2$, G$_1$). This also applies to the Jurassic bakevelliids described by Muster (1995) but may not be true for all Palaeozoic *Bakevellia*-like taxa.

Retroceramidae.—The multivincular Retroceramidae lack the calcitic prismatic ligamentat of the Inoceramidae and are in this respect more similar to the Isognomonidae, to which they were related by Crampton (1988), but as well to the Bakevelliidae. Nevertheless, the interspaces between resilifers are generally concave, and resemble a kind of second order resilifers (Crampton 1988: table 2). This is not the case in the postlarval specimens studied here. Unfortunately, larval and early postlarval shell stages of Retroceramidae are presently unknown.

It may be significant that the family is common in boreal environments of the Middle Jurassic. In contrast, the current specimens lived in relatively warm marine environments (Malchus and Steuber 2002).

Pulvinitidae.—The Pulvinitidae represent the fourth multivincular pterioidean taxon present in the Jurassic. New resilifers are said to be added exclusively anteriorly (Marshall 1998; Palmer 1984; Ward and Waller 1988). In fact, additions are basically irregularly alternating, even though most fibrous sublayers are added anteriorly (Malchus in press). If the larval shell figured by Marshall (1998: fig. 1) of a living species, *Pulvinites exempla* (Hedley), is representative of fossil Pulvinitidae, they differ from all prodissoconchs discussed here by their large P1 (L = 230 mm). There is also a clear growth interruption at about 330 microns length (if the P2/nepioconch boundary is indeed at 630 mm). The predominantly anteriorward growth of the adult liga-
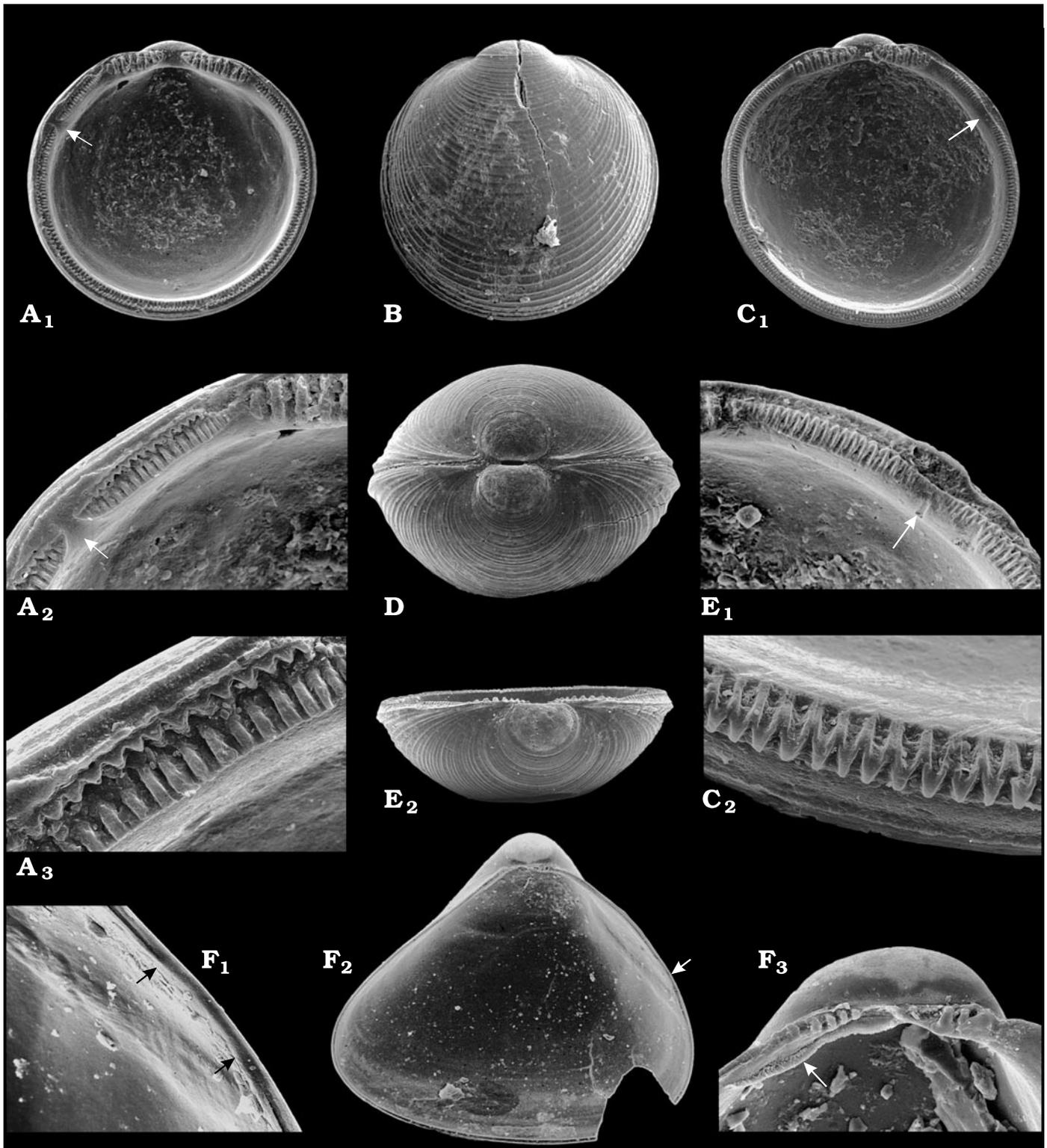
Fig. 5. **A–E**. Morphotype 9. **A**. P2-LV, arrows indicate pd-outlet, BGR X10868-7; A_1, entire valve, × 175; A_2, close up of dorsal-posterior segment with pd-outlet, × 500; A_3, close up of the two rows of gear wheel type, secondary denticles, typical of the LV, × 1250. **B**. P2, external; note that the valve was mounted before the significance of the pd-outlet was known; left or right cannot be established, therefore, BGR X10865-7, × 175. **C**. P2-RV, arrows indicate pd-outlet, BGR X10868-1; C_1, entire valve, × 175; C_2, close up of "gothic window frame" secondary denticles, × 1250. **D**. Articulated P2 valves viewed from back, left and right cannot be distinguished, BGR X10868-5, × 175. **E**. P2-RV, arrow indicates pd-outlet, BGR X10865-5; E_1, close up of posterior valve margin, × 500; E_2, entire valve from back, × 175. **F**. Pinnid (*?Atrina* sp.), recent, Mediterranean, P2-RV, BGR X10848-8; F_1, close up of posterior valve margin, note interruption (black arrows) of interlocking margin type, × 400; F_2, entire valve, arrow shows postion of pd-outlet, × 100; F_3, close up of hinge, arrow indicates detached position of resilium, growing anteriorly, × 400.

ment and the larval features make it unlikely that any of the morphotypes described here represents a pulvinitid species.

Non-multivincular Pterioidea.—Morphotypes 5 to 8 cannot be shown to be multivincular and nacreous as adults. Thus, in theory, they could represent any pterioidean taxon. However, larval shells of morphotypes 5 to 8 differ from those of non-multivincular Pterioidea by the same characters as described for the Isognomonidae (also compare, Bernard 1898: pl. 9: 9; Waller and Macintyre 1982: fig. 213a; Malchus in press). In addition, prodissoconch sizes of extant non-multivincular Pterioidea are ca. 30 percent smaller than those of M5 to M8 (Table 4). However, note that details of the larval hinge dentition and shell margin of living Pterioidea are still poorly known.

Ostreoidea.—Comparisons between larval shells of oysters and morphotypes 1 to 7 reveal extraordinary similarities. But oyster prodissoconchs are much smaller on the average (< 500 mm) (Palmer 1989; Malchus 1995, 2000b); they tend to reduce the anterior row of provinculum teeth (Malchus 2000b; Fig. $6B_2$); their left valves always possess a pd-notch and growth track (Waller 1981; Malchus 2000b; Fig. $6C_2$); and both the pd-notch of the left valve and thus also the pd-outlet of the right valve are much more dorsal, that is, nearer to the umbo than is the case for the morphotypes described here (compare, e.g., Figs. 1A, H_2, $2E_1$, $3H_1$ with $6B_2$–D). In addition, post-Triassic, adult oysters apparently lack nacreous shell layers (Carter 1990; McRoberts and Carter 1994; Hautmann 2001).

Pinnoidea.—Larval shells of extent pinnoidean bivalves share a rather characteristic, asymmetrically triangular outline with the anterior shell margin being straight, the anteroventral border elongated and narrowly rounded, and the shell being relatively weakly convex in cross section, (Miyazaki 1962: fig. 23; Booth 1979: fig. 1; Fig. $5F_2$). Booth (1979: 134) noted that the larval "ligament attachment point lies near anterior region of teeth" (see also Fig. $5F_3$).

It may be added that larval shells possess an interlocking shell closure and a posterodorsal interruption (Fig. $5F_1$, F_2), which is thought to be homologous with the pd-outlet of bakevelliids and oysters (see section "tuft organ and pd-outlet", below). These observations together with the general arrangement of provinculum teeth demonstrate that larval pinnoids are prosodetic, in contrast to their opisthodetic adult state. Remarkably, the larval ligament is below and detached from the anterior arm of provinculum teeth before it gently rises towards the anterodorsal shell margin (Fig. $5F_3$).

Morphotype 4 is morphologically and in terms of size similar to extant pinnid larvae (compare Table 3 and Fig. 3A–C with Booth 1979: 132, fig. 1). However, all specimens of morphotype 4 are more opisthogyrate, the number of teeth is higher, and the pd-outlet is closer to the hinge and smaller (compare Figs. $3A_2$, B_2 and $5F_1$, F_3). Nevertheless, the possibility cannot be excluded that some specimens included in M4 belong to the Pinnoidea rather than Bakevelliidae.

Taxa with a shell septum.—Morphotype 8 deviates from all other morphotypes in hinge characteristics and especially by the presence of a larval shell septum. As already mentioned in the descriptive part, a posterior septum is characteristic of adult Cassianellidae (Ichikawa 1958), *Lithiotis* (Chinzei 1982), and the bakevelliid genus *Kobayashites* (Cox, Newell, et al. 1969: N310). As the Cassianellidae are apparently restricted to the Triassic and the Lithiotidae to the Lower Jurassic, the Callovian morphotype 8 most likely belongs to the bakevelliid genus *Kobayashites*, even though this taxon is so far only known from the Bajocian of Japan and China (Muster 1995).

Taxa with larval gear-wheel shell margin.—Morphotype 9 is the only larval type known so far with this curious type of shell margin denticles. Its provinculum type suggests that it belongs to the Pteriomorphia, and the presence of a pd-outlet apparently indicates some relationship with the opisthogyrate Pterioida, whereas the shell shape, sculpture and symmetry of the hinge are more reminiscent of Jurassic Oxytomidae (Pectinoida). But, oxytomid prodissoconchs, preserved on early post-metamorphic shells, are thinner in cross section, and internal moulds of the valve margin lack any sign of shell margin denticles, even though a tongue-in-groove margin is clearly visible (Fig. 6K). Unfortunately, isolated larval shells of Oxytomidae have not yet been identified. Other taxa with an almost round and coarsely sculptured shell are found among Pycnodonteinae (Ostreoidea) and Pholadidae (Heterodonta), but their hinge characters are entirely different. Presently known larval shells of recent planktotrophic Limoida and Pinnoida are triangular (see above, and Fig. $5F_2$), and fossil and recent Arcoida are oval, with their length exceeding the height by at least 25 percent. Thus, a phylogenetic relationship with the Pectinoida presently appears the most likely.

Taxonomic distribution and evaluation of early ontogenetic characters

Developmental mode and prodissoconch types (characters A, B).—In order to evaluate characters D–G, J–O, and Q of Table 4 it is necessary to treat the developmental mode first (character A). This is because the above mentioned characters can only be present if there is a well developed prodissoconch 2 (P2), and this depends on the developmental mode. Note that only critical cases are discussed in more detail. Also note that developmental modes of fossil species are necessarily inferred from the prodissoconch itself (character B). The respective states of character A are therefore shown in brackets.

Currently available morphological evidence indicates that all fossil taxa (of Table 4), of which larval shells are known, developed planktotrophically. In addition, results of a stable isotope analysis of Malchus and Steuber (2002) suggest that

the Callovian bakevelliid larvae and the Kimmeridgian morphotype 9 were planktic. (Note that the two respective groups predominated in the analyzed larval shell samples. This was not specifically mentioned by the authors.) This result is not trivial because planktotrophy is not invariably correlated with planktic life (Chaparro et al. 2001, on *Tiostrea*). Doubts on the developmental mode mainly concern taxa with very large early ontogenetic shells (see character C, below).

Unpublished observations on Mediterranean *Musculus* spp. suggest that some Musculinae are at least partially planktotrophic. In the case of *Crenella*, direct observations are needed to clarify this matter (Ockelmann 1959: 50; Rees 1950: 91) because the presumed P2 shows a fine, antimarginal striation, which is a rather uncommon feature for a P2 of planktotrophic bivalves. A very similar striation also appears on the nepioconch of the Dacrydiinae and some Nuculidae. The striated portion in *Crenella* may represent the nepioconch, therefore, as was already suggested for other reasons by Rees (1950). Some Arcidae and Noetiidae are known to be planktotrophic developers (Odhner 1914; Loosanoff et al. 1966; Chanley and Andrews 1971). This may be true for most members of the group. Most living Pectinoida are also planktic-planktotrophic. A Jurassic example has been described by Malchus (2000a) (see Waller 1993, for an exception among recent Pectinidae).

Apparently, all Palaeotaxodonta develop by a (lecithotrophic) pericalymma stage, which differs from all other Bivalvia. The larval shell of most members of the group seems to mineralize late during larval ontogeny or shortly after metamorphosis (see Zardus and Morse 1998, for an overview). Early postlarval shells lack hinge teeth and a mineralized ligament. Nevertheless, commarginal growth bands, which generally indicate the P2 phase in planktotrophic taxa, are developed in some species (compare Gustafson and Lutz 1992; Gustafson and Reid 1986; Zardus and Morse 1998). It is currently not clear whether this shell type should be homologized with the P1 or both the P1 and P2, which would suggest that the veliger shell characteristics (including the hinge teeth) are homologous to palaeotaxodont juvenile shells.

Larval shell size (character C).—Full grown larval shells of bakevelliids measure more than 500 μm on the average and may reach 750 μm in length (or 845 mm, if specimen BGR BGR X10848-8, Fig. 5F$_2$, does not represent a pinnoid species) and are thus larger than any other supposedly planktic-planktotrophic Jurassic species studied so far (Malchus 2000a, b, c, d, and unpublished; Palmer 1989). It also exceeds the shell size of most planktic larvae of living species with some notable exceptions among the Mytiloida, for example, *Crenella* and *Solamen* (Ockelmann 1959; Zuschin and Oliver 2003), *Pinna* (Booth 1979), and fully lecithotrophic species such as in the Philobryidae (e.g., Hain and Arnaud 1992; Malchus and Linse, unpublished).

In contrast, large shell sizes between 500 and 2400 μm were apparently not uncommon among supposedly planktotrophic Palaeozoic cyrtodontid, praecardioid and lunulacar-

diid bivalves, and Cretaceous Inoceramidae (Dzik 1994; Knight and Morris 1996; Kříž 1966, 1996; Yancey and Heaney 2000; compare Fig. 6E–H).

The size distribution in Table 4 shows a general preference of certain size ranges within some higher taxa. Nevertheless, the evolutionary and/or autecological significance of large P2 sizes remains unclear. It is possible that the largest larvae were unable to stay in the plankton and were thus benthic. Yancey and Heaney (2000: 293, fig. 2) interpreted the large, early ontogenetic shell of the lunulacardiid *Buckhornia* as a juvenile stage. However, there are no other characteristics presently known to support this view.

The character is currently judged not informative for phylogenetic purposes.

Larval sculpture (character D).—In analogy to gastropods (Frank Riedel, personal communication 2001), the subordinate, commarginal growth increments of advanced P1 stages in bivalves could mark the moment when the larva begins to retract into the shell, even though the shell is not yet large enough to enclose the whole animal. This interpretation would explain the presence of commarginal growth lines on the prodissoconch of the entirely brood protected *Tiostrea chilensis* (Philippi) larvae (Ó Foighil et al. 1999: fig. 2a). The prominent, commarginal growth increments of the P2 stage probably indicate the onset of valve closure (Waller 1981). Waller (1981) also noted that the growth welts in living oysters are produced by the reflection of the mantle margin. This should also hold true for the taxa described here.

Growth welts apparently dominate over simple growth lines within taxa with opisthogyrate larval shells, that is, in the Bakevelliidae, Ostreoidea (especially Gryphaeidae), Pterioidea, Inoceramidae, and *Butovicella* (Knight and Morris 1996; Kříž 1966, 1996; Malchus 1995; Palmer 1989; Waller 1981; Waller and Macintyre 1982; this study, Figs. 2A, D, 3D, E, 4B, 6A, F). However, a cursory study of the taxonomic distribution of growth welts suggests that reflected mantle margins evolved many times independently, for example also in Pholadoidea, Anomiidae, Oxytomidae, and Arcoida (Boyle and Turner 1976; Malchus 2000c, d; Palmer 1989; present observations on Arcoida). Thus, the character is presently considered not informative for phylogenetic purposes.

Position of larval resilium at metamorphosis (character E).—Waller (1990) pointed out that the origination point of the larval ligament is quite variable in bivalves. My observations suggest that the origination point is specific for taxa above the family level. However, the origination point is often obscured by postlarval shell material. For this reason, it is here substituted by the "position of the larval resilium at metamorphosis". This position is apparently related to the onset and direction of helical growth, which varies considerably between higher taxa (Malchus in press, see also next section).

Spiral growth, growth direction of resilium, and repetitive ligament sublayers (characters F–I).—Growth and po-

sitioning of the ligament during ontogeny appear to follow five main rules departing from the position of the first resilium (character E; see Malchus in press for details).

(1) The growth direction of the ligament follows the general ontogenetic growth direction of the soft body (see section "opisthogyrate umbo and related terms", above) (character F).

(2) The first adult resilium is a continuation from the larval resilium. It therefore occupies the same relative (anterior, central or posterior) position on the hinge (character G).

(3) It follows from rule 1 that the ligament growth direction changes notably as soon as there is a drastic change in the general growth allometry during ontogeny. Typically, the most drastic change occurs either during growth of the first adult resilium or during the interval between the formation of the first and second resilium (if developed). However, note that the ontogenetic phase, during which such changes occur, as well as the direction of reorientation are not universally fixed but taxon-specific.

(4) The first and second postlarval resilia are plesiomorphically discontinuous in all Pteriomorphia (Waller 1990, 1998: 21; Malchus in press) (character H).

(5) Multiple lamellar and fibrous ligament sublayers (dupli- and multivincular ligaments, respectively) probably evolved by repetition of this initial discontinuity. However, in the course of evolution, repetitive ligaments became reduced again to the initial grade (e.g., in Anomiidae, Pectinoida, some Arcoida, some Pterioidea, Ostreoidea). Occasional re-appearances of multiple resilifers can be interpreted as atavisms (e.g., Ostreoidea) (character I).

The opisthogyrate bakevelliid morphotypes 1–8, oysters, Cretaceous inoceramids, Pinnidae, and the Silurian *Butovicella* share a larval prosodetic resilium (Knight and Morris 1996; Dzik 1994; Malchus 2000b, in press; Fig. 6E). In the opisthogyrate Pterioidea, the larval ligament at metamorphosis at least occupies an anterior position below the beak. Whether it grew anteriorly during the larval phase could not be observed. Where developed in this assemblage of taxa, postlarval second and further resilia are added posteriorly (Knight and Morris 1996; Dzik 1994; Malchus in press; this study). The Pulvinitidae are the only exception, as most resilia are added anteriorly (for details see Malchus in press).

In the prosogyrate Mytiloida, the larval fibrous ligament occupies a posterior or central position below the almost orthogyrate umbo. More pronounced helical growth begins somewhat later in ontogeny (Malchus in press). In general,

the first resilium is quickly abandoned after metamorphosis and substituted by the second, posteriorly extending ligament (e.g., Bernard 1898: pl. 4; Booth 1977; Dell 1987; Gustafson et al. 1998; Malchus in press; among many others). It is also noteworthy that some taxa like Dacrydiinae (Mytilidae) maintain a functional larval ligament into the adult stage, which then grows posteriorly, whereas the second adult ligament is not developed or vestigial (Ockelmann 1983). At least some species of *Crenella* (Crenellinae) show a reduction of the underlying pseudonymph which is otherwise typical of the Mytilidae.

Similar hinge types also characterize a number of Silurian and Devonian larval shells of supposed cyrtodont species (Dzik 1994: figs. 31, 36; Fig. 6G). However, left and right valves and therefore anterior and posterior orientation cannot be distinguished with certainty in these cases. Thus, strictly speaking, the direction of ligament growth is not determinable. One could only argue that the ligament should have grown posteriorly, because cyrtodonts are prosogyrate.

The Jurassic Oxytomidae, most Pectinidae, and Anomiidae develop only one postlarval fibrous ligament, which emerges from a central point on the hinge and extends ventralward (Malchus 2000a: fig. 2B, 2000c: fig. 2H, in press; Fig. 6I). However, in oxytomids, it continues to grow posteriorly. Assuming that the discontinuous ligament is an autapomorphy for the Pteriomorphia (Waller 1990; see above), the single resilium-character state must be an inherited resilium reduction from ancient ancestors of the respective lineages.

Many (or all?) planktotrophic Arcoida possess an approximately symmetrical larval hinge with a centrally or slightly posteriorly tending resilifer and fibrous resilium (present observations of Jurassic *Grammatodon* and living *Striarca*). In *Grammatodon* (Parallelodontidae), the resilifer is abandoned shortly after metamorphosis, whereas it becomes asymmetrically triangular in *Striarca* (Noetiidae) extending further posterior than anterior during early postlarval growth. Further development of repetitive fibrous and lamellar sublayers is distinct in the two families and also differs from ligament ontogeny in multivincular taxa, which are of main concern in the present study (further details on ligament grades in Carter 1990; Waller 1990, 1998; Malchus in press).

The Palaeotaxodonta were once believed to develop only one mineralized ligament which may be positioned posterior or anterior of the umbo (Waller 1990). In *Acila castrensis*

Fig. 6. **A, B**. P2 of *Nanogyra* sp. (Kimmeridge Clay, Westbury) **A**. LV from exterior, BGR X10865-1, × 150. **B**. RV, BGR X10867-1; B₁, internal view of → entire valve, arrow indicates position of pd-outlet, × 150; B₂, close up of dorsal valve margin, note reduction of anterior row of denticles and position of pd-outlet (arrow) very close to the umbo, × 200. **C, D**. P2 of *Neopycnodonte* sp. (recent, Mediterranean). **C**. LV, BGR X10858-8; C₁, arrow indicates internal track of pd-notch, × 175; C₂, arrow indicates external growth track of pd-notch, × 200. **D**. RV, arrow indicates internal growth track of pd-outlet, BGR X10858-7, × 175. **E–H**. Early ontogenetic shells of Silurian species. **E**. RV, early nepioconch of *Butovicella* cf. *migrans* (Barrande), arrow points at posterior row of hinge denticles below P1, Silurian, reproduced from Dzik (1994: fig. 32G), × 100. **F**: LV, juvenile or adult valve with P2 of *Butovicella migrans* (Barrande), reproduced from Kříž (1969), pl. 1: 1, × 75. **G**. RV(?) of a ?cyrtodontid P2 or juvenile shell, reproduced from Dzik (1994: fig. 31A), × 50. **H**. RV of a small adult *Butovicella migrans* (Barrande) with P2 largely preserved, reproduced from Kříž (1969: pl. 1: 6), × 25. **I**. *Anomia* sp., recent, Mediterranean. P2-LV, note interlocking type of shell margin, arrow points at position, where interlocking groove becomes slightly weaker, but it is not interrupted, BGR X10835-7, × 200. **K**. *Oxytoma* sp., Middle Jurassic, Kłęby. Umbonal part of adult with internal mould of P2 and remnants of P2 shell material (thick arrows), slender arrow indicates the positive mould of interlocking groove of larval shell, BGR X10857-2, × 200.
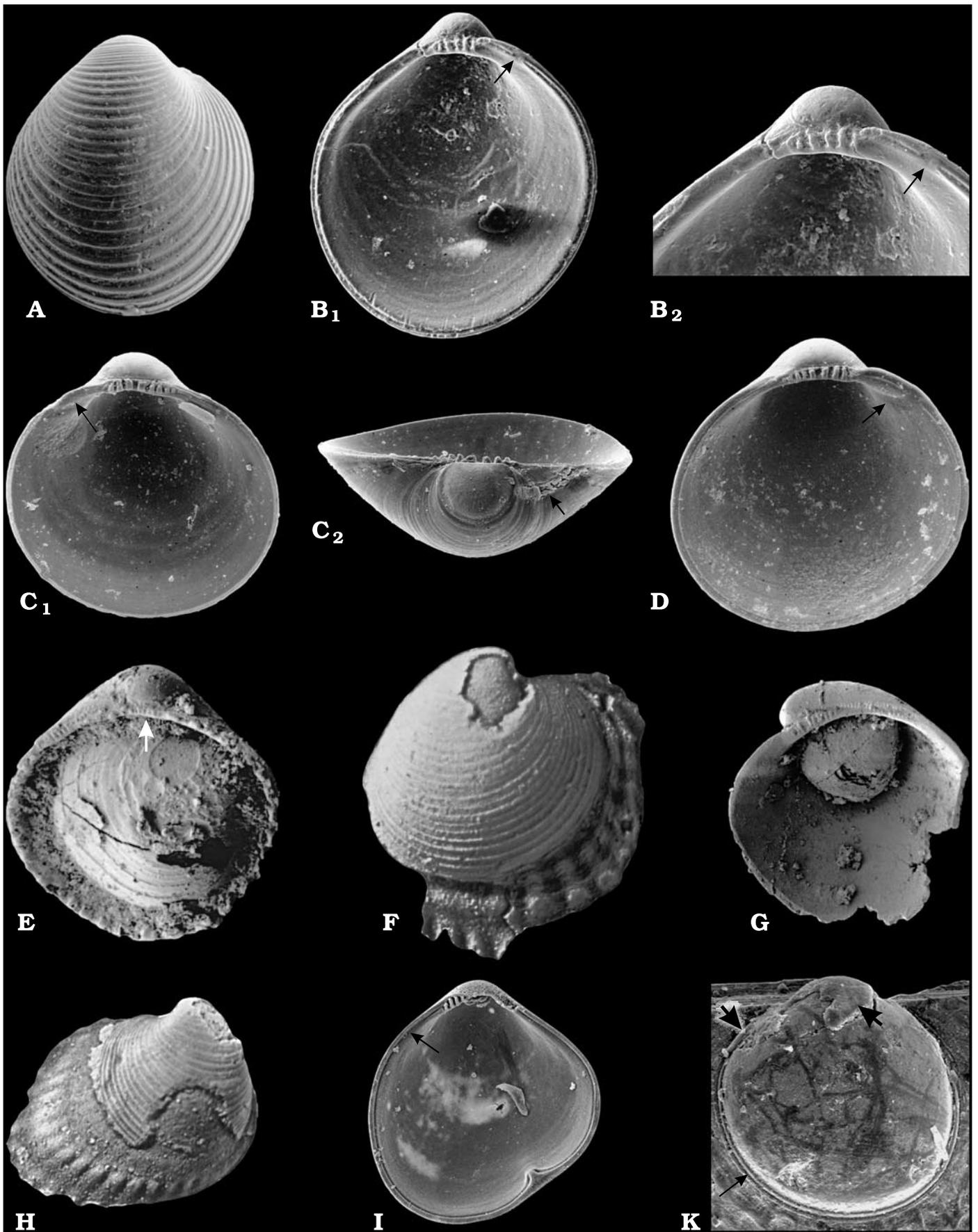
Table 4. Distribution of character states among the taxa discussed in the text (except Heteroconcha).

TAXA	A. developmental mode	B. P1/P2 boundary	C. larval shell size	D. larval sculpture	E. pos. larval resil. at metam.	F. growth dir. larval resilium	G. pos./growth dir.1st ad. resil.	H. position 2nd adult resilium	I. multiple adult lig. sublayers	J. larval valves interlocking	K. larval post-anal tuft	L. larval pd-outlet	M. larval pd-notch or pd-ridge	N. position outlet or notch	O. larval margin denticles	P. juvenile denticular structures	Q. larval septum	R. adult septum	S. nacre in adult shell
Acila [1]	0	0	0	0	?	?	(1)	0	0	(0)	1	(0)	0	(0)	(0)	0	0	0	0
Arca [2]	1	1	0	2	0	0	0	?	1D	?	?	?	?	-n-	?	0	0	0	2
Grammatodon [2]	1	1	0	2	0	0	0	?	4D	?	(1)	?	3	-n-	?	0	0	0	2
Mytilus [3]	1	1	0	0	0	0	0	1	2	0	?	0	0	-n-	0	1	0	0	0
Musculus [3]	1, 3	1	0	1	0	0	0	1	2	0	?	0	0	-n-	0	1	0	0	0
Crenella [3]	(2)	(2)	(1)	0	0	0	0	0	3	?	?	?	0	-n-	(0)	1	0	0	0
Cyrtodontids [4]	(1)	1	(1)	1, 2	(0)	(0)	?	?	?	(0)	?	?	0	?	0	(0)	?	0	0
Pecten [5]	1	1	0	0	1	0	1	0	0	0	?	0	0	-n-	0	0	0	0	2
Anomia/Juranomia [6]	1	1	0	1–2	1	0	1	0	0	1	(0)	0	0	-n-	0	0	0	0	2
Oxytoma/Meleagrin. [7]	1	1	0–1	2	1	0	2	0	0	1	?	?	0	?	(0)	0	0	0	2
M9 [8]	1	1	0	2	1	0	?	?	?	1	(1)	1	0	1	2	?	0	?	?
Butovicella [9]	(1)	1	1	2	2	1	(4)	0	0	?	?	?	0	?	?	0	0	?	?
Maida [10]	(1)	1	2	2	(2)	(1)	(4)	0	0	?	?	?	0	?	?	0	0	0	?
Inoceramidae [11]	(1)	1	2	2	2	1	(4)	1	1	?	?	?	0	?	?	0	?	0	0
?*Atrina* [12]	1	1	1	1	2	1	(4)	(1)	(2)	1	?	1	0	1	0	0	0	0	0
Bak M1–M2 [13]	(1)	1	1	1–2	2	1	4	1	1	1	(1)	1	0	1	0	0	0	0	0
Bak M3–M4 [13]	(1)	1	1	2	2	1	4	1	1	1	(1)	1	0	1	0	0	0	0	0
Bak M5, M7 [13]	(1)	1	1	2	2	1	(4)	?	?	1	(1)	1	0	1	1	?	0	0	?
Bak M6 [13]	(1)	1	1	2	2	1	(4)	?	?	1	(1)	1	0	1	0	?	0	0	?
Bak M8 (*Kobayash.*) [13]	(1)	1	(0)	1–2	2	(0)	(4)	?	?	1	(1)	1	0	1	0	?	1	?	?
Cassianella [14]	(1)	(1)	?	?	2	(1)	(4)	1	1	?	?	?	?	?	?	?	?	1	0
Lithiotis [15]	?	?	?	?	?	?	?	(0)	(0)	?	?	?	?	?	?	?	?	1	0
Pteria [16]	1	1	0	1–2	3	0	3	1	2	?	?	?	0	?	?	0	0	0	0
Electroma [16]	1	1	0	1–2	3	0	3	1	2	?	?	?	0	?	?	0	0	0	0
Malleus [16]	1	1	0	1–2	3	0	3	1	2	?	?	?	0	?	?	0,2	0	0	0
Vulsella [16]	(1)	(1)	?	(2)	?	0	(3)	?	?	?	?	?	0	?	?	0	0	0	0
Pinctada [16]	1	1	0	1–2	3	0	3	0	4	?	?	?	0	?	?	0	0	0	0
Isognomon [16]	1	1	0	1–2	3	0	3	1	1	?	?	?	0	?	?	0	0	0	0
Pulvinites [16]	(2)	2	(1)	1	?	(0)	(3)	3	1	?	?	?	?	?	?	?	?	0	0
Palaeolophidae [17]	?	?	?	?	?	?	(5)	?	5	?	?	?	?	?	?	0,2	?	0	1
Gryphaeinae [17]	(1)	1	0	2	2	1	5	0	4	1	(1)	1	1	2	0	0	0	0	1
Nanogyra [17]	(1)	1	0	2	2	1	5	0	4	1	(1)	1	1	2	0	2	0	0	2
Pycnodonteinae [17]	(1)	1	0	2	(2)	1	5	0	5	1	(1)	1	1	2	0	2	0	0	2
Cubitostrea [17]	(1)	1	0	1	2	1	5	0	4	1	(1)	1	1	2	0	2	0	0	2
Crass./Liost. [17]	1	1	0	1	2	1	5	0	5	1	(1)	1	1	2	0	0,2	0	0	2
Ostrea/Lopha [17]	2	1	0	1	2	1	5	0	5	1	1	1	1	2	0	2	0	0	2
Tiostrea [17]	3	0	0–1	0–1	3	(0)	5	0	5	2	(1)	2	2	-n-	(0)	2	0	0	2

Explanations to Table 4: Symbols: A to S, characters (details below). [1]Palaeotaxodonta: Nuculoidea; [2]Arcoida: Arcoidea; [3]Mytiloida: Mytiloidea; [4]Cyrtodontoida; [5] to [8]Pectinoida: [5]Pectinoidea, [6]Anomioidea, [7]Monotoidea; [8]Unknown affinity; [9] to [10]Praecardioida: [9]Butovicellidae, [10]Praeostreidae; [11]Ambonychioidea, [12]Pinnoida: Pinnoidea, [13] to [17]Pterioida: Pteriinae: [13]Bakevelliidae, [14]Cassianellidae, [15]Lithiotidae, [16]Pterioidea; [17]Ostreoida: Ostreoidea. 0, 1, 2, 3…, character states; (0), (1)…, inferred character states; "1–2" or similar, more than one character state realised in taxon; D, refers to duplivincular ligament grade; -n-, not applicable; ?, missing character information. **A**. Developmental mode: 0, test cell larva (pericalymma); 1, purely planktic-planktotrophic veliger; 2, lecithotrophic, partially planktic veliger; 3, planktic veliger stage very short or missing. Note that state A0 may be planktic, brooded or "direct" (Zardus and Morse 1998). Note, some *Musculus* and *Crenella* species may have other character states. **B**. Prodissoconch 1/2 boundary and ratios: 0, no clear boundary; 1, P1 < 100 μm, P1/P2 ratio < 0.4; 2, P1 generally > 90 μm, P1/P2 ratio 0.4–0.6; 3, P1 > 125 μm, P1/P2 ratio generally > 0.6 to ca. 0.9 (P2 is only fringe). Note that these values may not apply to all bivalves. **C**. Larval shell size: 0, smaller than 500 mm; 1, between 500 and 1000; 2, larger than 1000 mm. This refers to any shell present at the time of metamorphosis, irrespective of whether this is called prodissoconch 1 or 2. However, size comparisons of taxa with largely different

modes of development may be meaningless. Whether morphotype 8 gets much larger before metamorphosis is not known. **D**. Larval sculpture: 0, none to faint commarginal growth lines; 1, well developed but not prominent growth lines; 2, commarginal growth welts (reflected mantle margin) rather strong; 3, regular radial sculpture (faint). At present, comparisons may be considered valid between taxa with a true P2 stage. **E**. Position of larval resilium at metamorphosis: 0, posterior below larval umbo; 1, central below larval umbo; 2, anterior of larval umbo; 3, anterior below larval umbo. Note that not all species develop a resilium before metamorphosis. But there is generally a gap between the posterior and anterior denticle series, which is taken to indicate the future position of the mineralized ligament layer. **F**. Growth direction of larval resilium: 0, ventrally; 1, anteriorly (prosodetic). **G**. Position and growth direction of 1st adult resilium: 0, posterior below larval umbo, growth direction ventral; 1, central below larval umbo, growth direction ventral; 2, central below larval umbo, growth direction posterior (opisthodetic); 3, anterior below larval umbo, growth direction ventral or posterior (opisthodetic); 4, anterior of larval umbo, growth direction ventral; 5, anterior of larval umbo, growth direction anterior (prosodetic), later ventral. **H**. Position of 2nd adult resilium and growth directions: 0, absent; 1, posterior of 1st adult resilium (and larval umbo), growth direction posterior (opisthodetic); 2, as before but later change of growth direction to ventral (*Malleus*, *Vulsella*, etc.); 3, anterior of 1st adult resilium, growth direction ventral (*Pulvinites*) (prosodetic). Note, state 1 of Pinnoidea (?*Atrina*) requires confirmation. **I**. Multiple adult ligament sublayers: 0, originally absent; 1, always more than two present, 1D, duplivincular system (repetitive lamellar sublayers); 2, only the first two (adult) resilia developed, only the second remains functional (requires confirmation in ?*Atrina*); 3, as in state 2, but 1st and 2nd resilium are very close and almost fuse, pseudomymph vestigial (*Crenella*); 4, 2nd and further resilia always suppressed; 4D, there appears to be only 1 lamellar groove in *Grammatodon*; 5, occasionally developed (atavism or other). Note, D, duplivincular, all other examples refer to multivincular ligaments with repetitive resilia (fibrous sublayers). **J**. Interlocking larval valve margins: 0, absent; 1, present; 2, lost (owing to type of development). **K**. Larval post-anal tuft: 0, absent; 1, present. **L**. Larval pd-outlet: 0, absent; 1, present; 2, lost (owing to type of development). **M**. Larval pd-notch or pd-ridge: 0, absent; 1, pd-notch present; 2, pd-notch lost (owing to type of development); 3, pd-ridge present. **N**. Larval position of outlet/notch: 0, absent; 1, posterior; 2, posterodorsal. **O**. Larval margin denticles: 0, absent; 1, rectangular; 2, gothic window type. **P**. Juvenile denticular structures: 0, absent; 1, true secondary hinge dentition; 2, chomata. **Q**. Larval septum: 0, absent; 1, present. **R**. Adult septum: 0, absent; 1, present. **S**. Nacre in adult shell: 0, present; 1, present in some species or genera, but entirely reduced in most others; 2, constantly absent.

Hinds, it grows anteriorly (Zardus and Morse 1998). Note that palaeotaxodont ligaments are more diverse than can be discussed here (Carter 2001).

The assemblage of characters is apparently diagnostic at various taxonomic levels.

Interlocking valve margins (character J).—Interlocking (tongue-in-groove) larval valve margins, as described by Waller (1981) for *Ostrea edulis* L. are present in the Ostreoidea in general (see also Hu et al. 1993, all figures concerning larval shells), the bakevelliid morphotypes 1–8, ?*Atrina* (Pinnoidea), *Oxytoma* (Oxytomidae), *Anomia* (Anomiidae) (Malchus 2000c, d; this study), and Pholadoidea (Boyle and Turner 1976; Culliney and Turner 1976) (not shown in Table 4). This feature is of course unlikely to be present in larvae which cannot or do not close their shells such as *Tiostrea* and some (all?) Palaeotaxodonta ((Jozefowicz and Ó Foighil 1998: 432; Zardus and Morse 1998). At present, the character is of limited use for phylogenetic analyses. However, it becomes important in combination with the post-anal cilia tuft and posterodorsal shell characters (characters K–N).

Post-anal cilia tuft (character K).—A tuft of cilia in the anal region and dorsal to the anus appear in the larvae of many, phylogenetically distant species such as *Nucula* and *Acila* (Nuculoidea), *Ostrea* (Ostreoidea), *Teredo* (Pholadoidea), and others (see Waller 1981: 5, 62; and Zardus and Morse 1998, for more details and references). In addition, Gustafson and Reid (1986: 417) described a tuft of cilia protruding from the anus and a small cluster of post-anal cilia in the early post-larva of *Solemya reidi* Bernard. Interestingly, similar structures have not yet been reported from the Nuculanoidea, which share a basal dichotomy with the Nuculoidea and Solemyoidea (Carter et al. 2000; Waller 1998).

Morphology and function of these structures may represent autapomorphies in each species, as is claimed by Zardus and Morse (1998: 241) for *Acila castrensis* Hinds. However,

the taxonomic distribution is suggestive of a rather plesiomorphic root (Fig. 7). Although rather speculative at present, workers on bivalve larval anatomy have paid too little attention to these structures to reject this possibility without further investigation. A clarification of this matter would be interesting, considering the phylogenetic significance of larval shell characters L to N.

Posterodorsal shell characters (characters L–N).— Waller (1981) provided evidence that the posterodorsal notch (character M1) in *O. edulis* L.—plus its associated external growth track and internal interruption of the interlocking shell margin—coincides with the extrusion site of the post-anal cilia (character K). Although premordial stages of this ciliate organ already develop during the trochophora-like phase, the shell margin is not affected before the onset of valve closure (Waller 1981). The lack of a notch in the right valve was related to the fact that the anus is deflected to the left side in *Ostrea edulis*. This asymmetry is accompanied by the pronouncedly inequivalve larval shell of oysters (except for the long-brooding and equivalve *Tiostrea*).

Complementary studies of extant, Eocene and Jurassic oysters demonstrate that the interlocking valve margin (character J) is also interrupted in the right valves of oysters (character L; see Hu et al. 1993: figs. 1, 2, 6, 10, 14 on all right valves; Malchus 1995: pl. 4: A; Fig. 6B, D). The present study provides evidence that this interruption, here called "posterodorsal outlet" (new term) also characterizes left and right valves of morphotypes 1 to 8 (Bakevelliidae), morphotype 9 (? Pectinoida), and ?*Atrina* (Pinnoidea). In addition, Steffen Kiel (personal communication 2003) found that a number of Jurassic to recent Arcoida possess an external posterodorsal ridge in both valves (character M3). I could verify the presence of this feature in Jurassic *Grammatodon* and Recent *Striarca*. Because its position and antimarginal growth track are almost identical to the posterodorsal notch in oysters, Steffen Kiel suggested that the two characters

could be homologous. In fact, if this is correct, it must also be homologous to the posterodorsal outlet (see above). This leads invariably to the assumption that the presence of any of these shell structures indicates the presence of a post-anal tuft. As the larval shells of the studied morphotypes are equivalve (compare Fig. 2C), which also applies to the arcoids, the anus was probably in the plane of the commissure. This explains why bakevelliids, M9, ?*Atrina*, and the mentioned arcoids, in contrast to oysters, do not develop a posterodorsal notch.

Independent of their assumed homology, the pd-outlet/notch and ridge are useful features, because they indicate the posterior side of the larval shell and therefore allow the distinction of left and right valves (e.g., of morphotype 9), which would otherwise not be possible. As a corollary, they permit the orientation of the larval animal and localisation of the anus thus indicating that the anus lies much more dorsally in oysters than in morphotypes 1 to 9 or arcoids. It also proves that bakevelliid larvae are indeed opisthogyrate.

The phylogenetic significance of these shell characters largely depends on the assumed functional relation between tuft and notch/outlet or ridge. In theory, the outlet or ridge could be functionally related to the anus (and not to the tuft). In this case, these shell characters would just indicate the expulsion site of the faeces and the position of the anus. However, most bivalve larvae have an anus, whereas they lack a posterodorsal ridge or outlet. In addition, *Anomia* lacks a pd-outlet or notch despite their interlocking valves and a strongly inequivalve shell (Fig. 6I). It appears therefore rather likely that the posterodorsal shell structures are functionally related to the tuft.

Shell margin denticles (characters O, P).—The circumferential quadrangular and the gothic window-like marginal dentitions of morphotypes 5, 7, and 9 might have aided a tighter shell closure. This may therefore be a character of unprotected larvae. The Silurian *Butovicella* cf. *migrans* (Barrande) (Dzik 1994; Fig. 6E) and living species of *Crenella* also show crenulated, internal shell margins remotely similar to morphotype 5 and morphotype 7. However, these postlarval pseudo-denticles are related to the radial, external sculpture, which is lacking in the cited morphotypes. Early post-larvae of many Mytiloida develop a true second dentition before the adult hinge teeth are formed, and most Ostreoidea and some other pteriomorphian taxa develop chomata during their adult life (Malchus 1998). It is presently speculative, however, whether any of these structures are homologous. The quadrangular marginal denticles may constitute a symplesiomorphy for morphotypes 5 and 7, and the gear wheel type presently appears as an autapomorphy for morphotype 9.

Shell septa (characters Q, R).—This is the first study to describe a septum in a larval shell. Unfortunately, corresponding post-larvae are unknown. It is not possible, therefore, to prove the persistence of this septum in postlarval stages. However, the presence of a septum in a similar position in adult shells of some Bakevelliidae, all Cassianellidae and some Lithiotidae at least suggests that these features are symplesiomorphic homologues. The function of a septum in a larval shell remains enigmatic.

Nacre (character S).—The formation of nacre in post-metamorphic life stages is probably a basal plesiomorphy within the Pteriomorphia (Carter 1990). In the present context it is noteworthy that some of the phylogenetically and stratigraphically earliest oysters were partially nacreous (Hautmann 2001; McRoberts and Carter 1994).

Phylogenetic implications

For the following discussion, the data in Table 4 are converted into a more interpretative Table 5. Character A is maintained to show one (of many) basic differences between Palaeotaxodonta and Autolamellibranchia. Characters B to D and O, P are omitted because they are the least informative. Characters E and F are combined into character E' to emphasize the opisthogyrate character state of some larval shells. The information content of E' is similar to that of the original characters but is much more easily and more often observable. In addition, it includes important information on the ontogenetic timing of coiling. Characters L (pd-outlet) and M (pd-notch and ridge) appear in the combined character L'. Characters Q and R are combined in character Q'. This change implies that larval and adult septa are homologous, which requires further confirmation. Some character states of E', G, J, K and L' are plotted onto the phylogenetic tree of Fig. 7 (after Giribet and Wheeler 2002: fig. 8).

Assuming a functional relation between characters L' and K, the scattered taxonomic distribution of L'1 to L'3 suggests that the post-anal tuft (K1) is plesiomorphic at least for the taxa above the Mytiloidea if not for all Bivalvia (Fig. 7). However, note that the presence/absence of a pd-outlet in pholadids, which possess a tuft, needs confirmation as the figures in Boyle and Turner (1976) and Culliney and Turner (1976) are not sufficiently detailed. If the assumption is correct, the apparent lack of the tuft in many Pteriomorphia must reflect a reduction rather than the original character state. This interpretation reduces the importance of the character for phylogenetic inferences. But independent of this, the related shell characters are valuable at higher nodes (points 9 to 11, below).

Character state J1 (interlocking shell margins) within the Pteriomorphia may be restricted to taxa above the Arcoida. However, this is another tentative interpretation which requires more research. Interlocking valve margins are of course important as indirect evidence for the presence/absence of a post-anal tuft (see character state L'1).

The most intriguing characters are the larval opisthogyrate shell and its dependent ligament characters (E'4–6, G3–G5, Table 5, and Fig. 7). Their taxonomic distribution has a number of interesting phylogenetic implications.

Table 5. Distribution of character states modified from Table 4. For explanation of modifications see text. Symbols: E', G', K, L', Q', fused or otherwise modified characters with respect to Table 4; all other symbols see Table 4. **A**. Developmental mode: 0, test cell larva (pericalymma): 1, purely planktic-planktotrophic veliger; 2, lecithotrophic, partially planktic veliger; 3, planktic veliger stage missing or very short (few to 48 hours). Note that some *Musculus* species belong to character states 1 or 2. The state for *Crenella* species remains to be confirmed. **E'**. Time (ontogenetic stage) and direction of umbo coiling: 0, no early ontogenetic coiling; 1, larval stage: no or weak orthogyrate coiling, post-larval: ortho- to weakly prosogyrate; 2, larval stage: as in state 1, post-larval: pronouncedly prosogyrate; 3, larval stage: pronouncedly prosogyrate, post-larval: prosogyrate or not gyrate; 4, larval stage: opisthogyrate, post-larval: not gyrate; 5, larval stage: as state 4, post-larval: opisthogyrate state continues after metamorphosis; 6, opisthogyrate coiling lost due to developmental mode. **G**. Position and growth direction of 1st adult resilium: 0, posterior below larval umbo, growth direction ventral; 1, central below larval umbo, growth direction ventral; 2, central below larval umbo, growth direction first ventral, later posterior (opisthodetic); 3, anterior below larval umbo, growth direction ventral or posterior (opisthodetic); 4, anterior of larval umbo, growth direction ventral; 5, anterior of larval umbo (except *Tiostrea*), growth direction anterior (prosodetic), later ventral. **H**. Position of 2nd adult resilium and growth directions: 0, absent (or not applicable); 1, posterior of 1st adult resilium (and larval umbo), growth direction posterior (opisthodetic); 2, as before but later change of growth direction to ventral; 3, anterior of 1st adult resilium, growth direction ventral (prosodetic). **I**. Multiple adult ligament sublayers: 0, originally absent; 1, always more than two present, most of which remain functional; 1D, duplivincular type with repetitive lamellar sublayers; 2, only the first two (adult) resilia developed, only the second remains functional; 3, as in state 2, but the 1st resilium remains functional, 2nd resilium rudimentary or not developed; 4, 2nd and further resilia always suppressed; 4D, further lamellar sublayers suppressed; 5, occasionally developed (atavism or other). Note, apart from 1D and 4D, all examples refer to multiple resilia. **J**. Interlocking larval shell margins: 0, absent; 1, present; 2, lost (owing to type of development). **K**. Larval post-anal tuft: 0, absent; 1, present; 2, vestigial or lost. **L'**. Posterodorsal shell modifications: 0, absent; 1, outlets (both valves); 2, notch (left valve) and outlet (right valve); 3, ridge in each valve; 4, no shell modifications owing to long brooding; 5, lacking because of reduced tuft. **N**. Position of larval pd-outlet or notch: 0, posterior; 2, posterodorsal. **Q'**. Early ontogenetic septum: 0, absent; 1, present. **S**. Nacre in adult shell: 0, present; 1, present in some species or genera, but entirely reduced in most others; 2, constantly absent.

CHARACTERS / TAXA	A. developmental mode	E'. time and dir. of shell coiling	G. pos./growth dir. 1st ad. resil.	H. pos./growth dir. 2nd ad. resil.	I. multiple lig. sublayers	J. larval valves interlocking	K. larval post-anal tuft	L'. larval pd shell modifications	N. position outlet or notch	Q'. early otogenetic septum	S. nacre in adult shell
Acila [1]	**0**	0	(1)	0	0	(0)	**1**	(4)	-n-	0	0
Arca [2]	1	1	0	?	1D	?	?	?	-n-	0	2
Grammatodon [2]	1	1	0	?	4D	?	(1)	**3**	-n-	0	2
Mytilus [3]	1	2	0	1	2	0	?	0	-n-	0	0
Musculus [3]	1, 3	2	0	1	2	0	?	0	-n-	0	0
Crenella [3]	(2)	2	0	0	3	?	?	0	-n-	0	0
Cyrtodontids [4]	(1)	3	?	?	?	?	?	0	-n-	?	0
Pecten [5]	1	1	1	0	0	(2)	(2)	(5)	-n-	0	2
Anomia/Juranomia [6]	1	1	1	0	0	1	(2)	(5)	-n-	0	2
Oxytoma/Meleagrin. [7]	1	1	2	0	0	1	?	?	?	0	2
M9 [8]	1	1	?	?	?	1	(1)	1	0	0	?
Butovicella [9]	(1)	**4**	**(4)**	0	0	?	?	?	?	0	?
Maida [10]	(1)	**4**	**(4)**	0	0	?	?	?	?	0	?
Inoceramidae [11]	(1)	**4**	**(4)**	1	1	?	?	?	?	?	0
?*Atrina* [12]	1	**(4)**	**(4)**	1	2	1	(1)	1	0	0	0
Bak M1-M4 [13]	(1)	**4**	**4**	1	1	1	(1)	1	0	0	0
Bak M5-M7, M6 [13]	(1)	**4**	**(4)**	?	?	1	(1)	1	0	0	?
Bak M8 (*Kobayash.*)[13]	(1)	**(4)**	**(4)**	?	?	1	(1)	1	0	**1**	?
Cassianella [14]	(1)	**4**	**(4)**	1	1	?	?	(1)	?	**1**	0
Lithiotis [15]	?	?	?	(0)	(0)	?	?	(1)	?	**1**	0
Pteria, Electroma [16]	1	**4**	**3**	1	2	?	?	(1)	?	0	0
Malleus [16]	1	**4**	**3**	2	2	?	?	(1)	?	0	0
Vulsella [16]	(1)	**4**	**(3)**	2	?	?	?	(1)	?	0	0
Pinctada [16]	1	**4**	**3**	0	4	?	?	(1)	?	0	0
Isognomon [16]	1	**4**	**3**	1	1	?	?	(1)	?	0	0
Pulvinites [16]	(2)	**(4)**	**(3)**	3	1	?	?	(1)	?	?	0
Palaeolophidae [17]	?	?	**(5)**	?	5	?	?	?	?	?	1
Gryphaeinae [17]	(1)	**5**	**5**	0	**4**	1	1	**2**	**1**	0	1
Nanogyra [17]	(1)	**5**	**5**	0	**4**	1	1	**2**	**1**	0	2
Pycnodonteinae [17]	(1)	**5**	**5**	0	**5**	1	1	**2**	**1**	0	2
Cubitostrea [17]	(1)	**5**	**5**	0	**4**	1	1	**2**	**1**	0	2
Crass./Liost. [17]	1	**5**	**5**	0	**5**	1	1	**2**	**1**	0	2
Ostrea/Lopha [17]	2	**5**	**5**	0	**5**	1	1	**2**	**1**	0	2
Tiostrea [17]	3	**6**	**5**	0	**5**	2	(2)	**4**	-n-	0	2

(1) If the opisthogyrate larval shell evolved only once within the Pteriomorphia, character states E'3–6 link the Pterioida with opisthogyrate Praecardioida and thus suggest a so far unrecognised, basal phylogenetic split within the Pteriomorphia, which separates this group from all other major taxa such as Mytiloida, Pectinoida, Limoida, and Arcoida (Fig. 7).

(2) The inclusion of the Praecardioida in the opisthogyrate clade eliminates previous doubts of Carter (1990: 180), who retained the praecardioids as a separate order "pending further analysis of their relationship with the Arcoida". However, the Praecardioida remain paraphyletic unless one considers the opisthogyrate larval shell plus primary (not derived) single adult ligament a unique character set. So far the Butovicellidae, Praeostreidae, Antipleuridae, and Lunulacardiidae may be included in the Praecardioida (Tables 4, 5; Fig. 7). But only *Butovicella*, *Praeostrea*, and *Maida* (Butovicellidae and Praeostreidae, respectively) are doubtlessly opisthogyrate. Although this may also hold true for *Maminka*, Antipleuridae (see Liljedahl 1984: 73, emended diagnosis, and fig. 32F), it requires confirmation for the subfamily Vlastinae of the Antipleuridae (Cox, Newell, et al. 1969: 247) and the recently established genus *Buckhornia* (Yancey and Heaney 2000: 295) of the Lunulacardiidae. Opisthogyry of *Buckhornia* is based on my reinterpretation of Yancey and Heaney's (2000) description and figures, which coincides with previous interpretations of valve orientation by Clarke (1904) and Křiž and Serpagli (1993). Interestingly, the Lunulacardiidae appear in the Lower Ordovician and are therefore the oldest taxon of this assemblage.

(3) The present hypothesis suggests that all Pterioida are opisthogyrate. This includes the near-basal or basal Pterineidae and Ambonychioidea, which may have given rise to the Bakevelliidae and Pinnoidea, and the Inoceramidae, respectively (see review of phylogeny hypotheses, above). However, larval shells of Pterineidae are presently unknown and those of Ambonychioidea are only known if *Buckhornia* is indeed a lunulacardiid and if this family belongs to the Ambonychioidea as was suggested by Carter (1990: 204).

(4) The inclusion of a pinnid in the group of opisthogyrate taxa is noteworthy, because it allows its separation from the Mytiloida on the basis of independent evidence (compare Carter in press; Waller 1990). However, note that their opisthogyrate state is inferred from the anteriorward growing larval ligament and arrangement of hinge teeth (see above, and Fig. 7). The non-opisthogyrate umbo of recent species may represent either an ancestral or a derived state. But independent of this polarity problem, all shell data exposed in Carter (in press) and this study are consistent with results from recent genetic analyses, which link the Pinnoidea to the Pterioidea–Ostreoidea (Fig. 7; see review of phylogenetic hypotheses, above).

(5) The present hypothesis does not conflict with the two diverging placements of the Inoceramidae either within the Ambonychioidea of the Pterioida (Carter 1990) or with the Praecardioida (Johnston and Collom 1998). However, none of these potential ancestors has a multivincular ligament. It may therefore be that Inoceramidae derived from the Bakevelliidae or from a common ancestral group (?Pterineidae).

(6) The larval shell similarities are consistent with previous palaeontological evidence that bakevelliids gave rise to the Cassianellidae (characters E', G) as well as to the Pterioidea (at present only character E') (Ichikawa 1958; Carter 1990).

(7) The astonishing similarity between larval shell characters of the Bakevelliidae and Ostreoidea (characters E', G, L') confirms the hypothesis that the basically calcitic oysters evolved from prismatic-nacreous Pterioida (Carter et al. 2000) and invites the hypothesis that the Bakevelliidae belong to the stem line of the Ostreoidea. This view conflicts with Waller's (1998: fig. 4) hypothesis that oysters are more closely related to the Pectinoida (compare Fig. 7), but it is supported by genetic studies (Fig. 7; see review of phylogenetic hypotheses, above). In addition, some of the oldest representatives of oysters also preserve remnants of nacre (McRoberts and Carter 1994; Hautmann 2001), whereas nacre was lost in pectinoids long before the appearance of oysters.

(8) Character state E'4 links morphotype 8 (?*Kobayashites*) to the opisthogyrate group and character state Q'1 (shell septum) to the Cassianellidae and Lithiotidae (Table 5). The three taxa may therefore be closely related. This interpretation is consistent with Chinzei (1982) and Seilacher (1984), who advocated an evolutionary relation between the Bakevelliidae and Lithiotidae. Naturally, this is incompatible with Neveskaya's et al. (1971) hypothesis, who linked the Lithiotidae with the Ostreoidea and Chondrodonteidae (Neveskaya et al. 1971; see Carter 1990: 206ff, for more information). However, note that both hypotheses imply opisthogyrate larval shells for the Lithiotidae and Chondrodonteidae.

(9) The presence of a pd-notch and related features (characters L', N) clearly distinguish the Ostreoidea as a clade. But note that larval shells of the Palaeolophidae are not yet known (Malchus 2000b; Table 5, Fig. 7). From a larval-shell standpoint, only the presence of a pd-notch would identify them as true oysters.

(10) Modern Pterioidea appear to be monophyletic owing to character state G3 (Table 5, Fig. 7). Both monophyly hypotheses, for Ostreoidea and for Pterioidea, are supported by genetic studies (Campbell 2000; Steiner and Hammer 2000; Hammer 2001; Giribet and Wheeler 2002) (compare Fig. 7).

(11) Outside the opisthogyrate group, character state L'3 is potentially important for phylogenetic inferences within the Arcoida (Table 5, Fig. 7).

Conclusions

The present study demonstrates and enhances the utility of early ontogenetic shells of bivalves for anatomical orientation of isolated larval shells, taxonomy, questions of phylog-
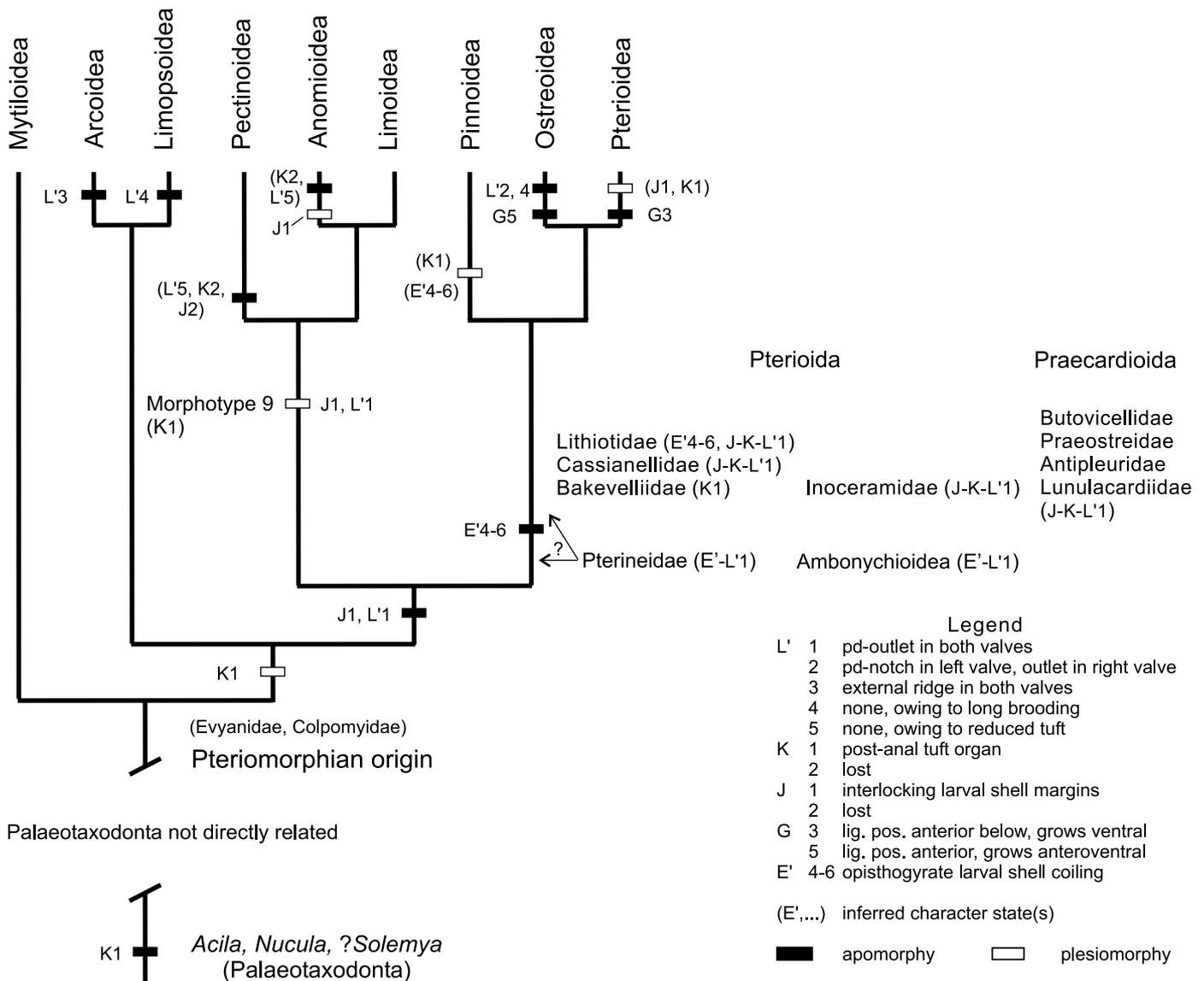
Fig. 7. Phylogeny hypothesis for the Pteriomorphia based on a combined analysis of genetic and morphological characters (after Giribet and Wheeler 2002: fig. 8; modified). The assumed position of larval key characters and of some fossil taxa are shown. Character states in brackets are based on indirect evidence from other character states, or, in the case of Pterineidae and Ambonychioidea, based on phylogeny hypotheses of Carter (1990). Character state L'4 of the Limopsoidea is suggested by observations of Malchus and Linse (unpublished).

eny, and character evolution. In addition, the phylogenetic interpretation put forward above allows predicting that larval shells of living Pterioidea possess prosodetic larval resilia, interlocking valve margins and pd-outlets. In case of functional relatedness, living Pterioidea, Pinnoidea and at least some Arcoidea (*Striarca* and relatives) should also have a post-anal tuft, whereas this character should be absent in the Anomioidea. These predictions can be easily tested, which would eliminate numerous question marks in the character matrices of Tables 4 and 5 and allow a better phylogenetic evaluation of these characters. With some effort, it should also be possible to find further direct evidence for the distribution of opisthogyrate shells and internal shell characters in fossil taxa.

The major problem with the present approach derives from the fact that the characters "larval opisthogyrate shell" and "posterodorsal shell characters" are plesiomorphic for most of the taxa treated here. At present, therefore, it makes little sense to analyze the data with a cladistic programme. The tuft and its supposedly related shell characters may even have a wider distribution than is currently known. Additional information is therefore needed to resolve early Palaeozoic nodes and those within the Pterioida. Future research in this field should seek answers to the following questions: What is the true distribution of opisthogyrate larval shells, interlocking valve margins, pd-outlet and ridge? And, are the various dorsal tufts plesiomorphically homologous, and are they functionally related to the pd-outlet and ridge?

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