

PALAEOBIOLOGY OF EARLY JURASSIC BAKEVELLIID BIVALVES FROM WESTERN CANADA

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ABSTRACT. Early Jurassic bakevelliid bivalves from the Canadian Cordillera are examined taxonomically, morphologically, and with respect to their biogeographical affinities. Four Early Jurassic species are recognized, which belong to the genera *Bakevellia*, *Gervillaria* and *Gervillella*. One species, *Gervillella leesi*, is new. In addition, *Gervillaria ashcroftensis* (Crickmay) from the Bajocian (Middle Jurassic) of British Columbia and the Lower Jurassic of northern Chile has been included in this study. A functional analysis of the morphologies of the five species reveals characteristic adaptations to distinct life habits. The spectrum comprises endobyssate sediment stickers, an orthothetically attached epibyssate form, and a twisted recliner. From Late Sinemurian to Late Pliensbachian times, the bakevelliid bivalves of the western Canadian allochthonous terranes, Wrangellia, Stikinia and Quesnellia, have strongest affinities to those from northern Chile and Argentina. During this time period Bakevelliidae appear to be absent from cratonal North America. This distributional pattern is consistent with a palaeogeographical position of the terranes closer to the South American Andes than previously assumed.

PALAEOBIOGEOGRAPHICAL studies of Jurassic benthic faunas have always suffered from a lack of detailed and reliable data from western North America. For this reason, one of us (MA) started to revise the Early Jurassic bivalve fauna from the western Canadian Cordillera. As this comprehensive revision is still in progress a palaeobiogeographical analysis of the whole bivalve fauna cannot be carried out at present. Here, we concentrate upon a particular group of benthic organisms, i.e. the bivalve family Bakevelliidae, with the main purposes (1) to document and revise taxonomically the Early Jurassic bakevelliids from western Canada; (2) to interpret their life habits by applying an analysis of functional morphology; and (3) to reconstruct the palaeobiogeographical distribution of the various species.

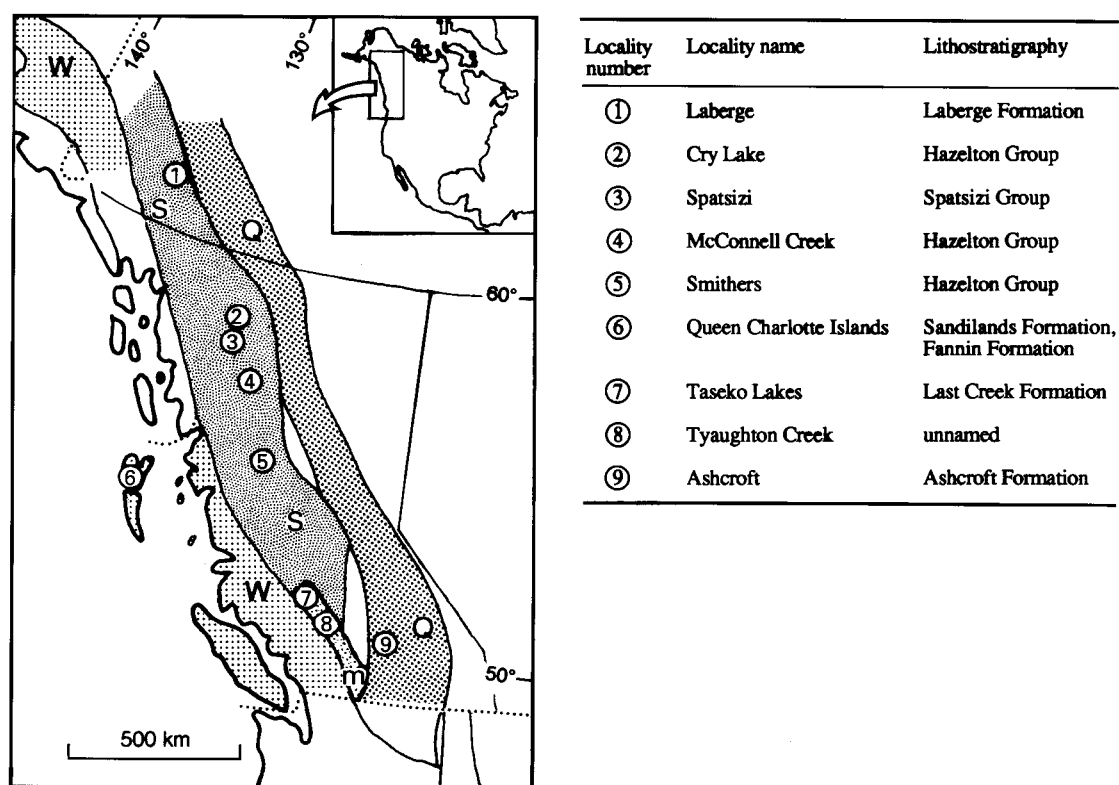
The endo- or epibenthic, byssally attached Bakevelliidae originated in the Late Permian, flourished during the Early and Mid Jurassic, and became extinct in the Late Cretaceous. They are characterized by a rhombic to trapezoidal outline with a more or less pronounced posterior wing. Ventral to a distinct ligamental area, which bears several ligamental pits, they exhibit various hinge teeth, which may vary considerably in number and shape. Bakevelliid bivalves have been selected here, because (1) they are relatively common benthic elements of Jurassic shelf seas; (2) they occur in a wide range of different lithofacies; and, most importantly, (3) they have been revised recently on the basis of an extensive survey of the published literature and careful examination of museum material (Muster 1995). This latter monograph provides a comprehensive and up-to-date data set that forms an excellent basis upon which to establish the palaeobiogeographical affinities of western Canadian bakevelliids with those from other regions.

GEOLOGICAL FRAMEWORK AND LOCALITIES

The western Canadian Cordillera consists of a collage of various tectonostratigraphical terranes, which were accreted to the western margin of the autochthonous North American craton (e.g. Coney *et al.* 1980). At what time these allochthonous terranes were accreted, and their relative

positions prior to docking are still open to debate. In addition to palaeomagnetic analyses, biogeographical data have been used also to place constraints on Early Jurassic palaeogeographical reconstructions of western North America (e.g. Taylor *et al.* 1984; Smith and Tipper 1986; Hallam 1994). We will test whether the distributional pattern of Early Jurassic bakevelliids is consistent with these reconstructions.

The localities which yielded bakevelliid bivalves are situated on three large terranes in British Columbia and southern Yukon. These terranes are, from west to east, Wrangellia, Stikinia and Quesnellia. Additional specimens are available from two small terranes (Cadwallader and Tyaughton terranes) from a tectonically complex region, the so-called 'Methow' Basin, in south-western British Columbia. Their relationships with other terranes are still controversial. Localities and their corresponding terranes are shown on Text-figure 1 and are listed in the Appendix.



TEXT-FIG. 1. Map of western Canada showing allochthonous terranes (stippled) and localities which yielded Early Jurassic bakevelliid bivalves. Allochthonous terranes: m, 'Methow' Basin; Q, Quesnellia; S, Stikinia; W, Wrangellia. Note that locality 7 lies on the Cadwallader Terrane and locality 8 lies on the Tyaughton Terrane.

MATERIAL AND METHODS

The taxonomic part of this study is based on the extensive Jurassic fossil collections of the Geological Survey of Canada housed in Calgary and Vancouver. In addition, type material of western Canadian bakevelliids figures by Crickmay (1930) and Lees (1934) has been examined. For comparison, Early Jurassic bakevelliid type specimens from northern Chile (Aberhan 1994), Argentina (Damborenea 1987; Muster 1995) and Europe (Muster 1995) were examined. Comparisons with other taxa as well as the establishment of geographical range data of species were

also aided by the recent revision of backvelliid bivalves (Muster 1995). All figured specimens from western Canada are deposited in the type collection of the Geological Survey of Canada, Ottawa, under the type numbers (prefix GSC) listed in the Text-figure captions.

SYSTEMATIC PALAEOONTOLOGY

Order PTERIOIDA Newell, 1965
 Family BAKEVELLIIDAE King, 1850
 Genus BAKEVELLIA King, 1848

Type species. *Avicula antiqua* Münster, in Goldfuss, 1836 (p. 126, pl. 116, fig. 7); by subsequent designation (King 1850, p. 166); Middle Muschelkalk; Glücksbrunn, Germany.

Subgenus BAKEVELLIA (BAKEVELLIA) King, 1848

Type species. As for genus.

Bakevellia (Bakevellia) waltoni (Lycett, 1863)

Text-figure 2D–G

- *1863 *Gervillia waltoni* Lycett, p. 110, pl. 32, fig. 4.
- v1934 *Gervillia* ? cf. *inflata* Schafh.; Lees, p. 42, pl. 4, fig. 2.
- v1934 *Bakevellia (Neobakevellia?) pintadae* Damborenea, p. 126, pl. 1, figs 1–5, text-fig. 4.
- v1994 *Bakevellia (Bakevellia) waltoni* (Lycett 1863); Aberhan, p. 16, pl. 2, figs 10–14, text-fig. 8.
- v1995 *Bakevellia (Bakevellia) waltoni* (Lycett 1863); Muster, p. 38, pl. 5, figs 1–13 [see for extensive synonymy list].

Material. Two left valves from GSC loc. 10246; one right valve from GSC loc. 19376; one left valve from GSC loc. C-81309; one left valve from GSC loc. C-81310; two left valves (GSC 112331 and GSC 112334) from GSC loc. C-81311; one left valve from GSC loc. C-81317; one left valve and one right valve (GSC 112333) from GSC loc. C-81322; three left valves and one articulated specimen from GSC loc. C-81323; one left valve from GSC loc. C-90924; one fragmentary right valve (GSC 112332) from GSC loc. C-90925; and one left valve from GSC loc. C-90930. Specimens are preserved as internal and external moulds; only in one specimen is relict shell material attached to the internal mould. For locality information see Appendix.

Occurrence. All records are from Stikinia; associated ammonites indicate a Sinemurian to Early Pliensbachian age.

Remarks. The most prominent features of *B. (Bakevellia) waltoni* are its rhombic shape; the presence of an acute anterior ear; a sharply pointed posterior wing; and a hinge consisting of one to four anterior teeth pointing in a postero-ventral direction and one or two elongated posterior teeth, which are oriented more or less subparallel to the hinge margin (Muster 1995). These characteristic features are also present in the studied specimens from western Canada.

Some specimens (e.g. Text-gig. 2F) exhibit external longitudinal grooves and ridges along the dorsal margin of the posterior wing. In this respect they superficially resemble *Pteroperna*, which also is bialate and has a sharply pointed posterior wing. Grooves and ridges along the dorsal margin, however, are also well known in *B. (B.) waltoni* (e.g. Muster 1995, p. 39, pl. 5, fig. 9). Whilst in *Pteroperna* the ridges appear to be related to the hinge, in *Bakevellia* they represent a thickening of the shell due to a concentration of growth lines in the region where the posterior wing becomes pointed. Furthermore, the main body of the shell of *Pteroperna* is more or less curved, whilst in *Bakevellia* it is always straight.

In contrast to *B. (Bakevellia) waltoni*, *B. (Bakevellia) binneyi* (Brown, 1841) exhibits a well rounded anterior auricle and the anterior teeth are arranged in a fan-like manner.



TEXT-FIG. 2. A-C-, H, *Gervillaria pallas* (Leanza, 1942). A, GSC 112327; GSC loc. 14333; internal mould of left valve with relict shell material attached; Pliensbachian, Dewar Peak, British Columbia; $\times 1$. B-C, H, from Joan Lake, British Columbia B, GSC 112328; GSC loc. C-90909; exterior view of left valve; lower Pliensbachian; $\times 1$. C, GSC 112329; GSC loc. C-103307; latex cast of left valve; Pliensbachian; $\times 1$. H, GSC 112330; GSC loc. C-103307; internal mould of right valve of articulated specimen (left valve figured on Text-fig. 2c),

Genus *GERVILLARIA* Cox, 1954

Type species. Modiola? alaeformis J. Sowerby (1819, p. 93, pl. 251); by original designation (Cox 1954, p. 49); Lower Cretaceous; Isle of Wight, Great Britain.

Gervillaria ashcroftensis (Crickmay, 1930)

Text-figures 3A–D, 5A–B

- v*1930 *Gervillia ashcroftensis* Crickmay, p. 48, pl. 3, figs a–c.
 v1994 *Gervillaria? ashcroftensis* (Crickmay 1930); Aberhan, p. 17, pl. 3, figs 3a–b, 4, text-figs 10–11.
 v1995 *Gervillaria? ashcroftensis* (Crickmay 1930); Muster, p. 53, pl. 9, figs 1, 2a–b, text-fig. 39.

Material. The holotype (GSC 25697) of *Gervillaria ashcroftensis* (Crickmay), which is an articulated specimen from GSC loc. C-186964.

Occurrence. The holotype is from the Bajocian of Ashcroft, British Columbia (Quesnellia).

Description. The shell is slightly twisted and sub-equivalved with the left valve being somewhat more inflated than the right one. The main body of the shell is relatively narrow and curved in a concave-up orientation with respect to the dorsal margin. The anterior part forms a more or less right angle with the plane of commissure. The beak is prosogyrate and almost terminal with a minute anterior auricle in front of it. The posterior wing is large and pointed at its postero-dorsal corner (as can be reconstructed from the growth lines).

The ligamental area exhibits up to six ligamental pits, which are always narrower than the interspaces between them (Text-figs 3B, D, 5A–B). The hinge of the holotype, which is an adult specimen, is completely crenulated. Nevertheless, individual teeth are still recognizable (Text-fig. 5A–B). The left valve (Text-fig. 5A) shows two anterior teeth, with the anterior one being considerably stronger; both are pointing in a postero-ventral direction. The posterior part of the hinge plate carries two elongated posterior teeth, which also point in a postero-dorsal direction. The corresponding right valve of the holotype (Text-fig. 5B) has a single anterior tooth, which is orientated in the same way as in the left valve. In a posterior direction follows at least one elongated posterior tooth. A second posterior tooth might have existed, but, due to intense crenulation in the posterior part of the hinge, is no longer recognizable. We interpret the triangular groove in front of the anterior teeth of both valves as a byssal groove (Text-fig. 5A–B). The pallial line consists of a series of irregularly spaced pits.

Remarks. Even though in western Canada *Gervillaria ashcroftensis* is only known from the Middle Jurassic (Bajocian), this taxon is relevant to our analysis of Early Jurassic bakevelliids, as it occurs in the upper Pliensbachian and Toarcian of northern Chile (Aberhan 1994). Until now the generic status of *G. ashcroftensis* could not be clarified on the basis of Crickmay's description and figures (Crickmay 1930, p. 48, pl. 3, figs a–c). In particular, too little information was available with respect to hinge characters. Therefore, we re-examined the holotype, which exhibits well the hinge in both the right and the left valve.

In the holotype, the slightly sub-equivalved and twisted nature of the shell, together with the complete crenulation of the hinge in adults, permit assignment of this species to *Gervillaria*.

Gervillaria pallas (Leanza, 1942)

Text-figure 2A–C, H

- v*1942 *Gervillia pallas* Leanza, p. 155, pl. 4, fig. 1.

Pliensbachian; × 1. D–G, *Bakevellia* (*Bakevellia*) *waltoni* (Lycett, 1863). D, F–G, from the Sinemurian of Mandanna Creek, southern Yukon. D, GSC 112331; GSC loc. C-81311; latex cast of shell interior of left valve; × 1.5. E, GSC 112332; GSC loc. C-90925; latex cast of hinge area of right valve; lower Pliensbachian, Joan Lake, British Columbia; × 1.5. F, GSC 112333; GSC loc. C-81322; composite mould of right valve; × 1.5. G, GSC 112334; GSC loc. C-81311; latex cast of left valve; × 1.5.



TEXT-FIG. 3. *Gervillaria ashcroftensis* (Crickmay, 1930). GSC 25697; GSC loc. C-186964; Bajocian of Ashcroft, British Columbia. A, exterior view of left valve. B, interior view of left valve. C, exterior view of right valve. D, interior view of right valve. All $\times 0.8$.

- 1987 *Gervillaria? pallas* (A. Leanza); Damborenea, p. 135, pl. 2, figs 1–5, text-fig. 7.
 1992 *Gervillaria(?) pallas* (Leanza); Damborenea, pl. 116, fig. 1a–b.
 1992 *Gervillaria? sp.*; Thompson and Smith, pl. 1, fig. 8.
 v1994 *Gervillaria pallas* (A. Leanza 1942); Aberhan, p. 18, pl. 4, figs 1a–b, 2a–b, 3a–b.
 v1995 *Gervillaria pallas* (Leanza 1942); Muster, p. 60, pl. 10, figs 3a–b, 4–5, text-fig. 43.

Material. One articulated specimen (GSC 112327) from GSC loc. 14333; one left valve from GSC loc. 19365; one left valve from GSC loc. 19373; one right valve from GSC loc. 19374; one articulated specimen from GSC loc. 19395; one left valve from GSC loc. 19397; three left valves, three right valves, and one articulated specimen from GSC loc. 19398; one left valve from GSC loc. 85333; one articulated specimen from GSC loc. 93327; one left valve from GSC loc. 93328; two left valves from GSC loc. C-53514; two left valves from GSC loc. C-81975; two left valves from GSC loc. C-90524; one left valve from GSC loc. C-90664; two left valves and one articulated specimen from GSC loc. C-90902; one left valve and one right valve from GSC loc. C-90903; six left valves and one articulated specimen from GSC loc. C-90905; one left valve (GSC 112328) and one articulated specimen from GSC loc. C-90909; one left valve from GSC loc. C-90924; four left valves and four articulated specimens from GSC loc. C-90925; three left valves from GSC loc. C-90926; three left valves from GSC loc. C-90928; one left valve from GSC loc. C-103198; two left valves from GSC loc. C-103305; and one left valve and one articulated specimen (GSC 112329, GSC 112330) from GSC loc. C-103307. Specimens are preserved as internal and external moulds; only rarely is relict shell material attached to the moulds. For locality information see Appendix.

Occurrence. See above. Associated ammonites indicate an Early Pliensbachian age on Stikinia and a Late Pliensbachian age on Wrangellia and Quesnellia.

Remarks. *Gervillaria pallas* is characterized by a strongly inequivalved and twisted shell, the left valve being strongly convex, the right valve concave. It exhibits a small anterior ear and a pointed posterior wing. By the presence of two carinae in the left valve, which extend from the umbo to the postero-ventral region of the shell, *G. pallas* can be distinguished from all other Jurassic *Gervillaria* (see also Muster 1995).

Gervillaria pallas was originally described from the Pliensbachian of Argentina (Leanza 1942) and more recently has been documented in detail from the Pliensbachian and Toarcian of Argentina and Chile (e.g. Damborenea 1987; Aberhan 1994). The morphological features of the studied specimens from western Canada agree well with those of their South American counterparts.

In the Canadian specimens, the width of the double carina remains relatively narrow, whilst in South American specimens it commonly widens in adults, although narrow double carinae are known as well (e.g. Damborenea 1987, pl. 2, fig. 4). Therefore we regard this to be a relatively variable feature within a single species.

Genus *GEVILLELLA* Waagen, 1907

Type species. *Perna aviculoides* J. Sowerby, 1814 (p. 147, pl. 66); by subsequent designation (Cox 1940, p. 112); Oxfordian; Osmington (near Weymouth), Great Britain.

Gervillella leesi sp. nov.

Text-figures 4A–E, 5D

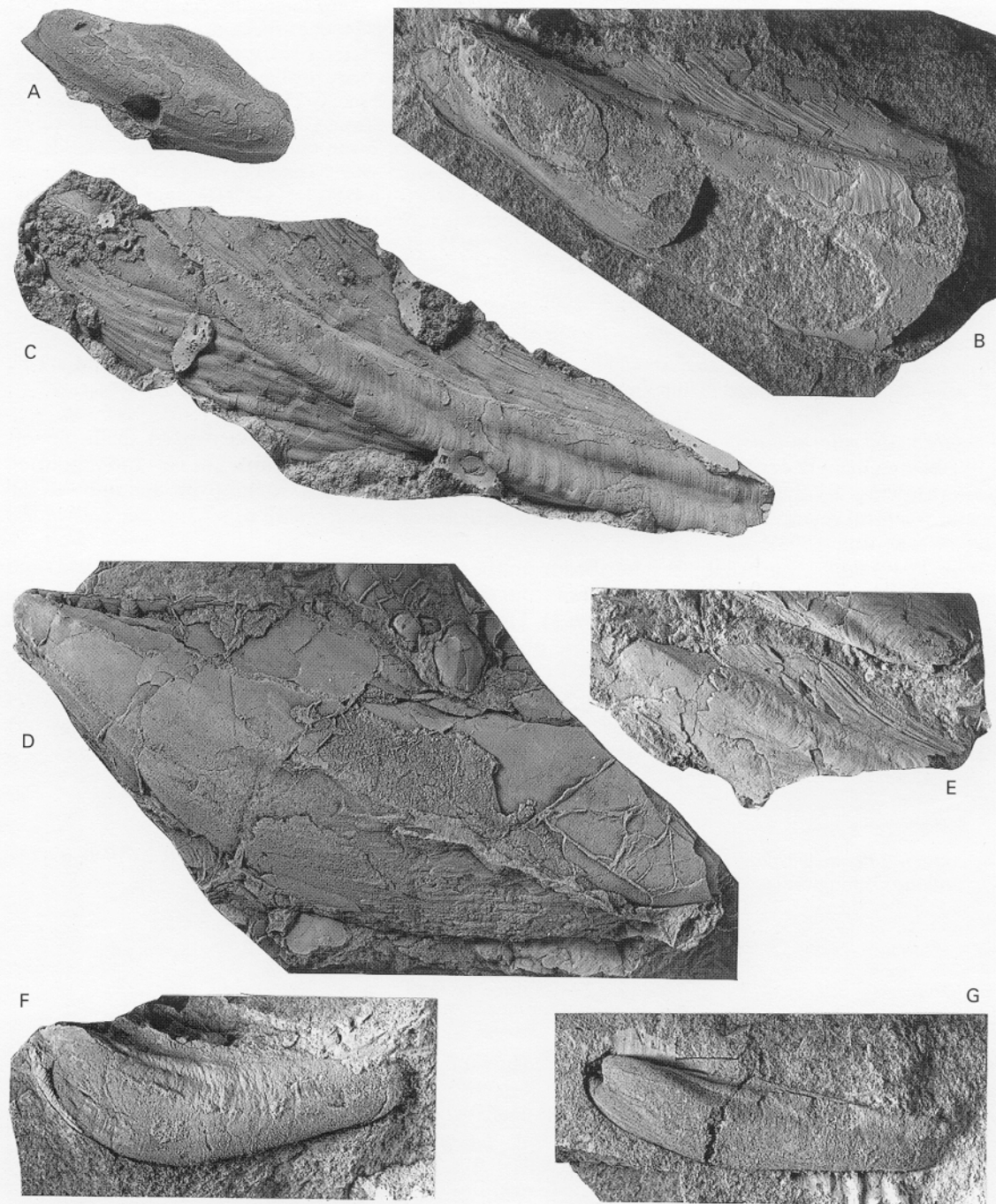
v1934 *Gervillia* sp. nov. Lees, p. 41, pl. 4, fig. 1.

Derivation of name. After Everett J. Lees, who recognized this as a new species.

Holotype. GSC 112324, left valve, figured in Text-figure 4E.

Type locality. Probably upper Sinemurian of Hunter Basin, between Webster and Goathorn creeks, Telkwa Mountains, 54° 31' N, 127° 05' W, Smithers map-area, British Columbia (GSC loc. 84187).

Additional material. Two left valves and one articulated specimen (GSC 112321) from GSC loc. 83995; one articulated specimen from GSC loc. 83998; three left valves from GSC loc. 84187; two left valves and one articulated specimen from GSC loc. 88495; five left valves (including GSC 112322) from GSC loc. 88602; one left valve from GSC loc. 88604; five fragmentary valves from GSC loc. 94993; four left valves (including GSC 112323) from GSC loc. 95015; three left valves and one right valve from GSC loc. C-143287;



TEXT-FIG. 4. A-E, *Gervillella leesi* sp. nov. A, GSC 112320; GSC loc. C-157663; internal mould of left valve; Hettangian, Tyaughton Creek, British Columbia. B, GSC 112321; GSC loc. 83995; left valve of articulated specimen; upper Sinemurian, Babine Lake, British Columbia. C, GSC 112322; GSC loc. 88602; latex cast of left valve; upper Sinemurian, Telkwa Mountains, British Columbia. D, GSC 112323; GSC loc. 95015; internal mould of left valve; Sinemurian, McBride River, British Columbia. E, GSC 112324; GSC loc. 84187; exterior

and one left valve (GSC 112320) from GSC loc. C-157663. Specimens are commonly fragmented and preserved as internal and external moulds; rarely is relict shell material attached to the moulds. For locality information see Appendix.

Occurrence. See above. Associated ammonites indicate a Late Sinemurian age on Stikinia and a Hettangian age on the Tyaughton Terrane.

Diagnosis. Subequivalved *Gervillella*; double carina running from umbo to postero-ventral corner of shell on both valves and delimiting main body of shell from posterior wing; shell not twisted.

Description. Medium-sized, elongated shell; not twisted. Posterior part of main body slightly curved upwards. Angle between dorsal margin and vector of maximum growth 25 to 30°. Subequivalved, left valve being slightly more convex than right one. Dorsal margin straight, occupying nearly half the shell length.

Anterior ear small and pointed, limited from main body by shallow sulcus. Posterior wing large, obtuse, its posterior margin being slightly concave.

Two well-rounded carinae extend from umbo to postero-ventral corner of shell on both valves. More ventrally placed carina slightly stronger and coinciding with maximum inflation of shell; more dorsally placed carina clearly separates main body of shell from posterior wing. Shallow sulcus present between the two carinae. Carinae developed as shell thickenings and only weakly preserved in internal moulds.

Ligament multivincular. Ligamental area exhibits at least five ligamental pits. Interspaces between them are narrower than pits in anterior half of ligamental area; in posterior direction interspaces increase in width and finally became wider than pits. Hinge poorly known; internal mould of a left valve (Text-fig. 4D) exhibits elongated groove, which is impression of one posterior tooth. Posterior tooth starts below the third ligamental pit and is orientated slightly oblique to dorsal margin.

Outer surface of shell covered by conspicuous growth lines, which bend abruptly when meeting carinae.

Remarks. Within the Bakevelliidae, the presence of one or two carinae is confined to only a few species (*Gervillaria pallas*, *Gervillella araucana* and *Gervillella leesi* sp. nov.), which today are found along the western margin of North and South America. In contrast to *G. leesi*, *G. pallas* is strongly inequivalved and twisted, less elongated, and exhibits a pointed posterior wing. Similarly, *Gervillella araucana* can be separated from *G. leesi* by being inequivalved and twisted. Moreover, it carries only one carina on the left valve and is more strongly elongated.

Gervillella araucana Damborenea, 1987

Text-figures 4F–G, 5C

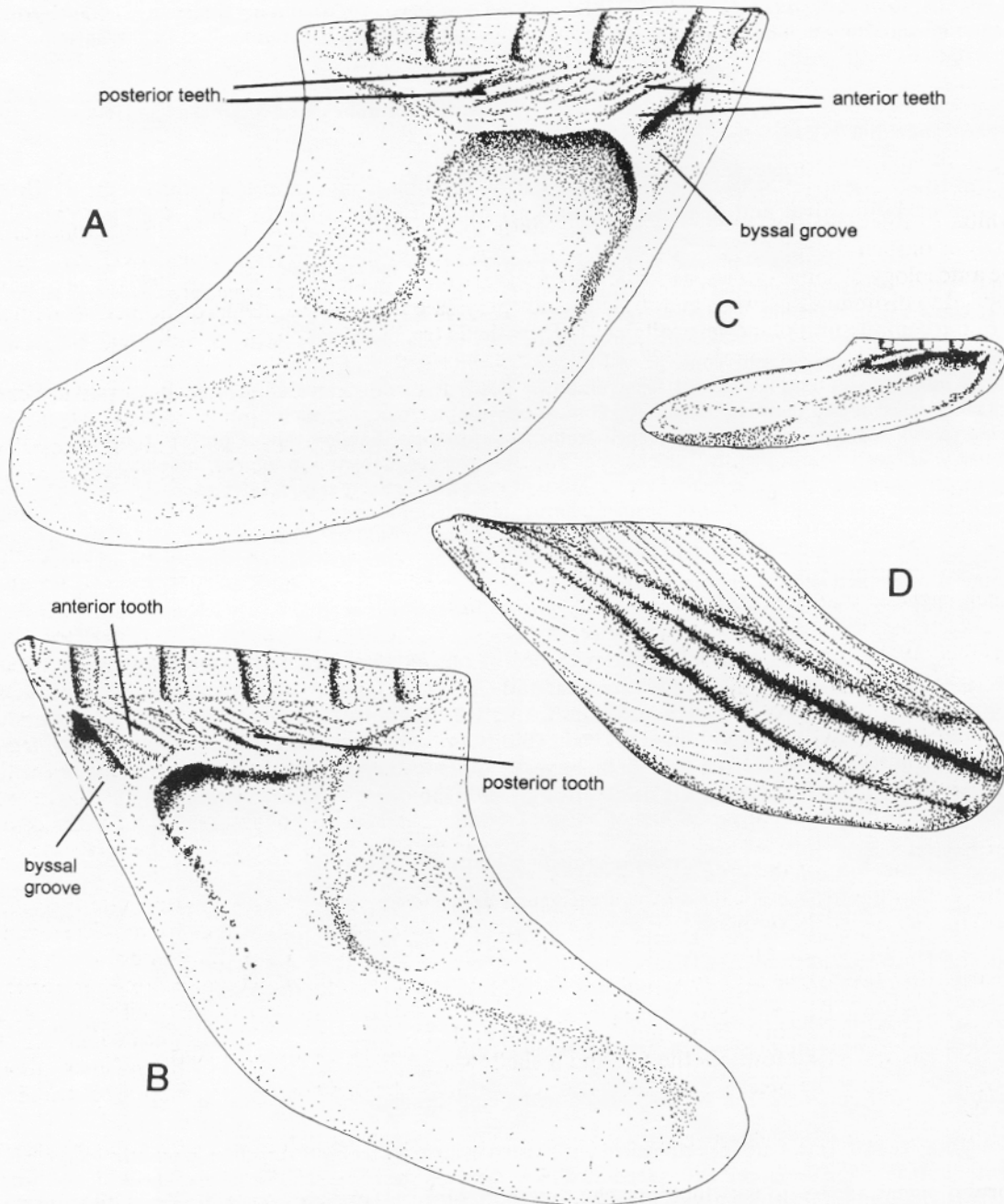
- *1987 *Gervillella araucana* Damborenea, p. 133, pl. 1, figs 6–10, text-fig. 6.
- v1994 *Gervillella araucana* Damborenea 1987; Aberhan, p. 18, pl. 3, figs 8–10.
- v1995 *Gervillella araucana* Damborenea 1987; Muster, p. 61, pl. 12, figs 3–4.

Material. Three left valves from GSC loc. 85335; two left valves (GSC 112325 and GSC 112326) from GSC loc. 88495. Specimens are preserved as internal moulds. For locality information see Appendix.

Occurrence. All records are from Stikinia; associated ammonites indicate a Late Sinemurian age.

Description. The left valves are very elongated and twisted in an anti-clockwise direction in posterior view. The anterior auricle is well developed and is separated from the main shell by a shallow sulcus. The posterior wing is narrow and obtuse. It is delimited from the main shell by a carina which extends from the umbo to the postero-ventral corner and which is followed ventrally by a shallow sulcus. An internal mould of a left valve (Text-figs 4G, 5C) shows the impression of a short anterior tooth and an elongated posterior tooth, both pointing downwards in a posterior direction.

view of left valve; upper Sinemurian, Telkwa Mountains, British Columbia. All $\times 1$. F–G, *Gervillella araucana* Damborenea, 1987; GSC loc. 88495; Upper Sinemurian, Babine Lake, British Columbia. F, GSC 112325; internal mould of left valve. G, GSC 112326; internal mould of left valve. Both $\times 1.5$.



TEXT-FIG. 5. Reconstructions of Jurassic bakevelliid bivalves from western Canada. A–B, *Gervillaria ashcroftensis* (Crickmay, 1930). A, interior view of left valve. B, interior view of right valve. C, *Gervillella araucana* Damborenea, 1987; interior view of left valve. D, *Gervillella leesi* sp. nov.; exterior view of left valve.

Remarks. *Gervillella araucana* is well known from the Lower Jurassic of South America (e.g. Damborenea 1987; Aberhan 1994) and the studied Canadian specimens cannot be distinguished from South American material.

Gervillella araucana can be separated from all other *Gervillella* by the presence of a single carina, which is only developed on the left valve.

FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

As the youngest known bakevelliid bivalves are of Late Cretaceous age, a direct ecological comparison of fossil with Recent forms is not possible. However, the five species described above exhibit distinct shell features, which allow interpretation of their mode of life from a functional analysis of their morphology. Although this approach might lead to an erroneous interpretation of the autecology of some species, as a rule the results are fairly reliable (e.g. Fürsich 1980). The criteria applied to distinguish between endobysate and epibysate life styles as well as orthothetic (oriented with the commissural plane vertically) and pleurothetic (reclining on one side) shell orientations are basically those used by Stanley (1972) and Seilacher (1984).

The inferred life habits of Early Jurassic bakevelliids from western Canada are illustrated in Text-figure 6. *Bakevelliia* (*Bakevelliia*) *waltoni* is reconstructed in a semi-infaunal, endobysate living position with the sagittal plane more or less vertical as is typical for most known species of *Bakevelliia*. This interpretation is based on the nearly equivalved condition, the presence of an anterior auricle, and the absence of appreciable flattening of the ventral margin as well as lack of extensive shell thickening.

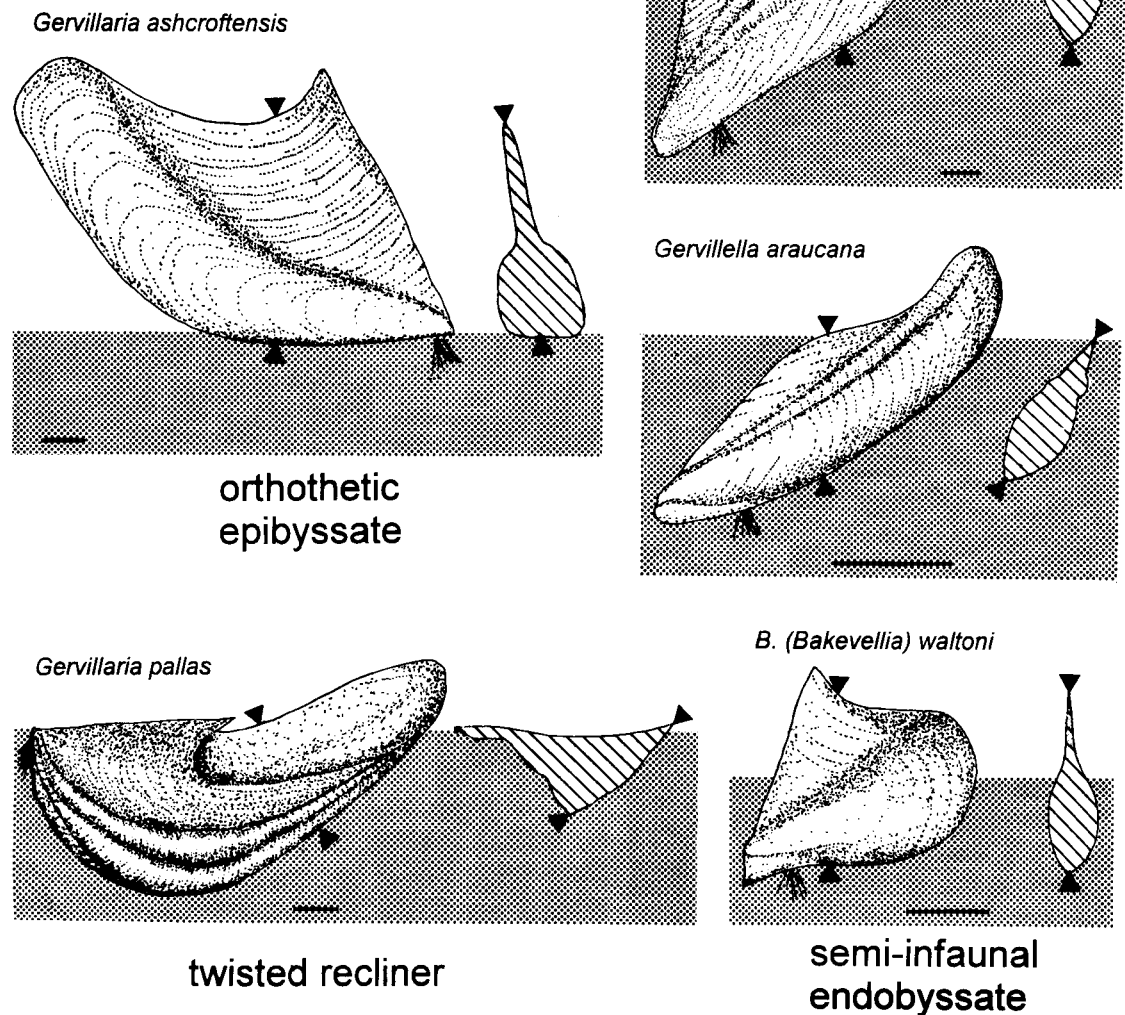
A similar endobysate mode of life can be inferred for *Gervillella leesi*. In addition to the morphological criteria just mentioned, *G. leesi* exhibits a relatively elongate, retrocurved shell form, which suggests that the species was buried more deeply.

In contrast, *Gervillaria pallas* corresponds well to the paradigm of a twisted recliner (see also McGhee 1978; Savazzi 1981; Damborenea 1987). A highly inequivalved shell and differential thickening of the cup-shaped lower valve in the umbonal region suggest that stabilization in relatively soft substrates was maintained by shape and weight. Adhesion to the sediment was probably increased by the presence of a pair of carinae on the left valve. Furthermore, the large, strongly pointed posterior wing substantially extended the left valve area, which was in contact with the sediment. Due to the strong torsion of the shell, the postero-ventral end emerged above the substrate forming a low angle with the sediment-water interface. Although there is no evidence of a byssal gape, a weak byssus, emerging between the valves at the anterior margin, might have added to the stabilization of the shell.

In terms of morphological characters, *Gervillella araucana* occupies an intermediate position between *Gervillella leesi* and *Gervillaria pallas*. Its elongate form, presence of a well-developed, lobate anterior auricle and lack of ventral flattening suggest a semi-infaunal, endobysate life position. A weak byssus probably emerged in the antero-ventral region, where the anterior auricle is separated from the main body of the shell by a shallow sulcus on the left valve. Shell torsion and reduction in the convexity of the right valve were probably associated with a slight inclination of the commissural plane towards the left and a shallower position of the shell in the sediment than in *G. leesi*. Again, the presence of a posterior carina in the left valve may have helped to stabilize the shell.

Whilst the species discussed above were either adapted to a semi-infaunal or a reclining mode of life, equipped with an, at best, weakly developed byssus, *Gervillaria ashcroftensis* displays morphological adaptations, which are characteristic of an epibysate mode of life, with a nearly vertical position of the sagittal plane. These adaptations include (1) the nearly equivalved condition of the shell; (2) a marked thickening of the shell in the umbonal and hinge region of both valves; (3) the presence of a very minute anterior auricle and therefore almost terminal beaks; and (4) antero-ventral flattening of both valves, which lowers the centre of gravity and provides a broad surface for epifaunal fixation. To our knowledge, *G. ashcroftensis* is the only species of the family Bakevelliidae which, presumably, was orthothetically attached to firm and stable substrates with a byssus and the ventral margin resting on the substrate. Therefore, the bakevelliid lineage appears

LIFE HABITS OF
BAKEVELLIIDAE
FROM THE JURASSIC
OF WESTERN CANADA



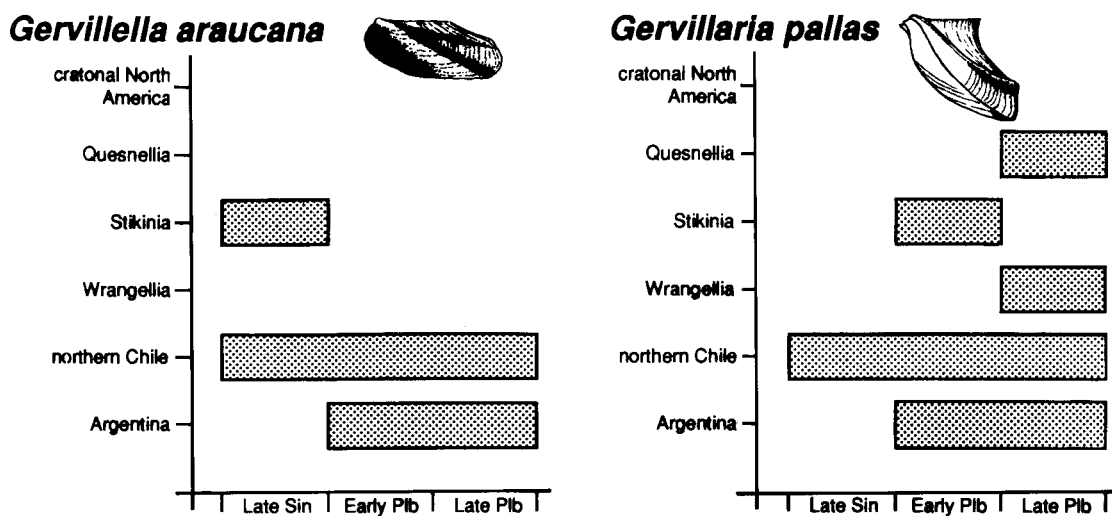
TEXT-FIG. 6. Life habits of bakevelliid bivalves from the Jurassic of the western Canadian Cordillera. Represented are three semi-infaunal, endobyssate sediment stickers, one orthothetically attached, epibyssate form, and one twisted recliner. Reconstructions of life habits are based on an analysis of functional morphology. Scale bars represent 10 mm. For explanations see text.

to be another example in which early forms were endobyssate and epibyssate habits, including that of the pendent *Gervillia*, arose later in phylogeny. This well established evolutionary trend has been documented primarily in Palaeozoic bivalves (Stanley 1972; see also Seilacher 1984).

PALAEOBIOGEOGRAPHICAL AFFINITIES

Distribution of Early Jurassic bakevelliids

The biogeographical distribution of fossil taxa is often plotted on palaeogeographical maps. As the history of the western North American terranes is still debated, however, we refrained from this kind of graphical representation. On the other hand, to plot data points on a present-day geographical map provides a more objective and geologically neutral frame of reference, but fails to illustrate the actual spatial relationships between different areas for various time periods. In the following, we prefer therefore to comment briefly on the spatial distribution of Early Jurassic bakevelliids. In addition, we illustrate area-time charts for two biogeographically interesting species (Text-fig. 7).



TEXT-FIG. 7. Temporal distribution of two conspicuous Early Jurassic bakevelliid bivalves along the eastern Pacific margin. Sin, Sinemurian; Plb, Pliensbachian. Note the faunal similarity between South America and western Canadian allochthonous terranes and the absence of bakevelliids from cratonal North America.

Bakevellia. On a global scale, two species of *Bakevellia* have been recognized from the Lower Jurassic: *B. (B.) waltoni* (Lycett) and *B. (B.) binneyi* (Brown). Both occur in mid palaeolatitudes in sediments ranging from fine- to coarse-grained siliciclastics to carbonates. The former appears to have been more widespread, with records from central Europe, Japan, western South America and western Canada (Stikinia). *B. (B.) binneyi* has been reported only from central Europe and Japan (e.g. Muster 1995).

Gervillaria. Of the five species of *Gervillaria* recognized by Muster (1995) four are known from the Lower Jurassic. *G. ashcroftensis* is reported from the Pliensbachian and Toarcian of northern Chile (Aberhan 1994) and occurs later in the Bajocian of British Columbia, Canada (Crickmay 1930). Similarly, *G. pallas* appears to be restricted to the eastern Pacific margin (Text-fig. 7) being recorded from the Sinemurian and Pliensbachian of northern Chile (Aberhan 1994), the Pliensbachian of Argentina (Damborenea 1987) and from the Pliensbachian of western Canada (Quesnellia, Stikinia and Wrangellia). Both occur in more or less calcareous siltstones, fine- to medium-grained sandstones, and mud- to wackestones. Two further species, *G. alaeformis* (J. Sowerby) and *G. hartmanni* (Münster) have been documented from central Europe and northern Chile, the former

also from Japan (e.g. Aberhan 1994; Muster 1995). Again, both species occur in a wide range of sedimentary rocks including shales, marls, sandstones, and wacke- to packstones.

Gervillella. Another bakevelliid, which currently is known only from regions along the eastern Pacific margin, is *Gervillella araucana*. In South America (Argentina, northern Chile) it is represented in rocks of Sinemurian to Pliensbachian age (Damborenea 1987; Aberhan 1994). In the Stikinia terrane of western Canada, *G. araucana* is known from the Sinemurian (Text-fig. 7). The preferred substrates of *G. araucana* were silts to fine-grained sands and what are now packstones. *Gervillella leesi* from the Hettangian of Tyaughton Creek and the Sinemurian of Stikinia appears to be endemic to western Canada, where it is preserved in more or less calcareous siltstones to coarse-grained sandstones. Two further species of *Gervillella*, *G. aviculoides* (J. Sowerby) and *G. lanceolata* (Müster) are confined to the Lower Jurassic of central Europe.

Aguilerella and *Gervillia*. Early Jurassic representatives of *Aguilerella* and *Gervillia* appear to be absent from western Canada and have relatively restricted distributions elsewhere (see Muster 1995). The Late Sinemurian or Pliensbachian specimens from north-western Canada figured as *Aguilerella* sp. by Poulton (1991, pl. 9, figs 1–4, 10–11) are too poorly preserved to allow identification at the generic level.

Andean affinities

According to their palaeogeographical distribution, the five western Canadian bakevelliid species described above can be assigned to one of the following categories: (1) cosmopolitan (*B. (Bakevellia) waltoni*); (2) endemic to western Canada (*Gervillella leesi*); and (3) restricted to the eastern Pacific margin (*Gervillaria ashcroftensis*, *Gervillaria pallas*, *Gervillella araucana*). Taxa unique to a single sample area and those with a cosmopolitan distribution do not add any information with regard to areal relationships and are not considered further. This also applies to *G. ashcroftensis*, which seems to have been confined to northern Chile during the Early Jurassic. In contrast, *G. araucana* and *G. pallas* are more widely distributed, occurring in several areas along the eastern Pacific margin (Text-fig. 7).

Clearly, our data set is too small to test seriously different terrane reconstructions, but it is interesting to see how it matches with existing models. For this purpose it is necessary to compare the terrane fauna with that from regions with a fixed position relative to the allochthonous terranes. Such areas are the stable craton of western North America ranging from the north-western margin of the Canadian Arctic Islands, northern and eastern Yukon, through the Fernie Basin of north-eastern British Columbia and south-western Alberta, and finally into the United States (e.g. the Sonomia terrane in Nevada, which had accreted to the continent by the Triassic). In the southern hemisphere, Chile and Argentina may serve as stable reference areas for the Early Jurassic.

The distributions of ammonoids (Smith and Tipper 1986) and of the pectinid bivalve genus *Weyla* (Damborenea and Manceñido 1979; pers. obs.) both indicate that the terranes Wrangellia, Stikinia and Quesnellia were in the eastern rather than the western Pacific during the Early Jurassic. This is consistent with the distribution pattern of bakevelliids. Besides their occurrence on the terranes, both *G. araucana* and *G. pallas* were found only in autochthonous western South America (Text-fig. 7). This clearly indicates eastern Pacific affinities and seems to support the idea of a West American bivalve province during the Early Jurassic as postulated by Hallam (1977). Smith and Tipper (1986) also suggested that the terranes were in the northern hemisphere by the Pliensbachian. If correct, we would expect higher similarities in the bivalve fauna of the terranes to those of cratonal North America rather than to those of South America. However, there is not one unambiguous record of an Early Jurassic bakevelliid from the North America craton (pers. obs.; see also Smith *et al.* (1994) for a compilation of illustrated Lower Jurassic bivalves from North America). In part, lack of suitable facies may account for this pattern. Although bakevelliids generally occur in a wide range of different substrates (see above), the Early Jurassic black shales

and dark-coloured calcareous mudstones of the Fernie Basin suggest unfavourable, oxygen-poor benthic environments. Moreover, the Early Jurassic bivalve fauna of the Western Interior of the USA is sparsely documented and the apparent lack of bakevelliids may be due to collection failure. Alternatively, the Late Sinemurian to Late Pliensbachian distributional pattern of bakevelliids is also consistent with a position of the terranes closer to the South American Andes, possibly even in the southern hemisphere.

Other bivalves which appear to be restricted to western South America (Chile, Argentina) and the terranes Wrangellia, Stikina and Quesnellia during the Early Jurassic are found, for example, among the pectinaceans. The Hettangian through Toarcian genus *Weyla* is by far the most abundant element in these regions, in terms both of number of individuals and especially, biomass. At least four species of *Weyla* appear to be restricted to these two regions. A detailed biogeographical analysis of Early Jurassic pectinoid bivalves along the eastern Pacific margin is being prepared by one of us (MA) and will provide further clues as to the palaeogeographical history of western Canadian terranes.

Acknowledgements. We thank F. T. Fürsich for critically reading the manuscript and A. Seilacher for a stimulating discussion of functional morphology in bivalves. T. P. Poulton and H. W. Tipper provided access to the collections of the Geological Survey of Canada in Calgary and Vancouver respectively. H. Schirm and B. Rutley carried out the photographic work. In part, the study was financially supported by a post-doctoral grant of the Deutsche Forschungsgemeinschaft (Fu 131/17-1). Finally, we thank S. R. A. Kelly and an anonymous referee for their careful reviews of the manuscript.

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Typescript received 13 March 1995
Revised typescript received 20 July 1996

APPENDIX

List of GSC fossil localities in the Canadian Cordillera yielding bakevelliid bivalves. Details include, where available, collector; year; field number; name and short description of locality; NTS: 50000 scale topographical map reference number (with name of 1:250000 scale map sheet in brackets); latitude; longitude; terrane; and age. All collections are deposited in the Geological Survey of Canada.

- GSC locality 10246. E. J. Lees; 1930; Laberge area; NTS 105 E(Laberge); Stikinia; (?) Sinemurian.
- GSC locality 14333. C. S. Lord; 1945; FT28d; 3.3 km south of Dewar Peak; NTS 94 D(McConnell Creek); Stikinia; Pliensbachian.
- GSC locality 19365. J. A. Jeletzky; 1950; Seal Point; NTS 92 E(Nootka Sound); Wrangellia; Late Pliensbachian.
- GSC locality 19373. J. A. Jeletzky; 1950; 116/6; Liver Point; NTS 92 E(Nootka Sound); Wrangellia; Late Pliensbachian.
- GSC locality 19374. J. A. Jeletzky; 1950; 100/36; Seal Point; NTS 92 E(Nootka Sound); Wrangellia; Pliensbachian.
- GSC locality 19376. J. A. Jeletzky; 1950; 115/7; Liver Point; NTS 92 E(Nootka Sound); Wrangellia; (?) Pliensbachian.
- GSC locality 19395. J. A. Jeletzky; 1950; 100/56c; Seal Point; NTS 92 E(Nootka Sound); Wrangellia; Late Pliensbachian.
- GSC locality 19397. J. A. Jeletzky; 1950; 122/1; Mushroom Point; NTS 92 E(Nootka Sound); 49° 55' 30" N; 127° 12' 10" W; Wrangellia; Early Jurassic.

- GSC locality 19398. J. A. Jeletzky; 1950; 122/4; Hoadley Point; NTS 92 E(Nootka Sound); Wrangellia; Early Jurassic.
- GSC localities 83995 and 83998. H. W. Tipper; 1969; F7TD-1s and F8TD-4s; small island north-east of Showshoe Island on Babine Lake; NTS 93 L(Smithers); 54°54'45" N; 126°10'05" W; Stikinia; Late Sinemurian.
- GSC locality 84187. H. W. Tipper; 1969; F19TD-6; Hunter Basin, between Webster and Goathorn creeks, Telkwa Mountains; NTS 93 L(Smithers); 54°31' N; 127°05' W; probably Late Sinemurian.
- GSC locality 85333. H. W. Tipper per R. Park; 1970; J6-17-HF; south-west end of Sterret Island on Babine Lake; NTS 93 L(Smithers); 54°55' N; 126°11' W; Stikinia; probably Early Pliensbachian.
- GSC locality 85335. H. W. Tipper per R. Park; 1970; 20-70P-2F-TD; tiny island south of south-west end of Sterret Island on Babine Lake; NTS 93 L(Smithers); 54°55' N; 126°10' W; Stikinia; Late Sinemurian.
- GSC locality 88495. T. P. Poulton; 1971; PU-24-71-2F; small island south of Sterrett Island on Babine Lake; NTS 93 L(Smithers); 54°54' N; 125°10'18" W; Stikinia; Late Sinemurian.
- GSC locality 88602. T. P. Poulton; 1971; PU-40-71-27F; head of Houston Tommy Creek, Telkwa Mountains; NTS 93 L(Smithers); Stikinia; Late Sinemurian.
- GSC locality 88604. T. P. Poulton; 1971; PU-43-71-1F; Telkwa Mountains; NTS 93 L(Smithers); Stikinia; probably Late Sinemurian.
- GSC localities 93327 and 93328. H. W. Tipper; 1975; F5T-13TD-75 and F14-13TD-75; Dewar Peak; 56°42'30" N; 126°47' W; NTS 94 D(McConnell Creek); Stikinia; Early Pliensbachian.
- GSC locality 94993. H. W. Tipper; 1977; F8-6TD-77; 20 km south-east of Turnagain Lake; NTS 104 I(Cry Lake); 58°9' N; 128°58'30" W; Stikinia; Late Sinemurian.
- GSC locality 95015. H. W. Tipper; 1977; F2-17TD-77; 10.5 km west of McBride River; NTS 104 I(Cry Lake); 58°10' N; 129° W; Stikinia; Sinemurian.
- GSC locality C-53514. H. W. Tipper; 1978; 78-TD-ASH-4B; Rattlesnake Hill, north of Ashcroft; NTS 92 I(Ashcroft); 50°46' N; 121°13' W; Quesnellia; Late Pliensbachian.
- GSC localities C-81309, C-81310, and C-81311. T. P. Poulton; 1979; east of Mandanna Creek; NTS 105 E(Laberge); 61°44' N; 135°41' W; Stikinia; Sinemurian.
- GSC locality C-81317. T. P. Poulton; 1979; east of Mandanna Creek; NTS 105 L(Glenlyon); 62°00'07" N; 135°48' W; Stikinia; Sinemurian.
- GSC localities C-81322 and C-81323. D. Templemen-Kluit; 1979; east of Mandanna Creek; NTS 105 E(Laberge); 61°44' N; 135°41' W; Stikinia; Sinemurian.
- GSC locality C-81975. H. W. Tipper; 1979; 79TD-219FA; Joan Lake; NTS 104 H(Spatsizi); 57°29'30" N; 128°55'00" W; Stikinia; Early Pliensbachian, Ibex Zone.
- GSC locality C-90524. H. W. Tipper; 1981; 81(TD)56)11; south side of Joan Lake anticline, Joan Lake; NTS 104 H(Spatsizi); 57°28'22" N; 128°56'15" W; Stikinia; Early Pliensbachian.
- GSC locality C-90664. H. Gabrielse; 1981; 81-GA-31-1; 10.5 km north-north-west of headwaters of Conglomerate Creek, Eaglenest Range; NTS 104 H(Spatsizi); 57°29'50" N; 128°56' W; Stikinia; Early Pliensbachian.
- GSC localities C-90902, C-90903, C-90905, C-90909, C-90924, C-90925, C-90926, C-90928, and C-90930. H. W. Tipper; 1981; 81-TD-5-2a, 81-TD-5-3a, 81-TD-5-3c, 81-TD-52-3A, 81-TD-53-5a, 81-TD-53-4c, 81-TD-53-4B, 81-TD-53-3b, and 81-TD-53-1a; 0.4 km west of Joan Lake camp; NTS 104 H(Spatsizi); 57°29'55" W; 128°54'12" W; Stikinia; Early Pliensbachian.
- GSC locality C-103198. H. W. Tipper; 1985; 83-TD-39F; south of Nation Peak; NTS 104 H(Spatsizi); 57°37'50" N; 128°53'30" W; Stikinia; Early Pliensbachian, Frebaldi Zone.
- GSC localities C-103305 and C-103307. H. Gabrielse; 1983; 83-GAT-4c and 83-GAT-5b; Joan Lake; NTS 104 H(Spatsizi); 57°29'15" N; 128°53'20" W; Stikinia; Early Pliensbachian.
- GSC locality C-143287. H. W. Tipper; 1986; 22B-F; south-west of Cardtable Mountain and south of Relay Mountain, Tyaughton Creek; 51°05'14" N; 122°59'05" W; NTS 920/2; Tyaughton Terrane; Late Hettangian.
- GSC locality C-157663. H. W. Tipper; 1984; 306a; Tyaughton Creek area; NTS 920/2; Tyaughton Terrane; Hettangian.
- GSC locality C-186964. C. H. Crickmay; 1926; east slope of Semlin Hill, north of Ashcroft, locality 6 in Crickmay (1930); NTS 92 I(Ashcroft); Quesnellia; Bajocian.