



On the Steinmanellidae (Bivalvia: Myophorelloidea); their palaeobiogeography, evolution and classification

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With 7 figures

Abstract: The trigoniid group “Pseudo-Quadratae” was introduced for Cretaceous descendants of Myophorellidae with a convergent resemblance to Tethyan Quadratotrigoniinae (= Quadratae). Subsequently it was made the basis of the subfamily Steinmanellinae, which herein is elevated to family rank. The earliest record of the group is from the Early-Middle Kimmeridgian of the Tethyan Realm (American Province), from where it spread into the Boreal and Gondwanic realms. Steinmanellids rose to dominance in the cool temperate waters of the Andean Province, and the latter represents their centre of diversification. They are absent from the predominantly cold circum-polar waters of Southern and Eastern Gondwana, i.e. the Antarctic and Maorian provinces, as well as from the Australasian Province. The evolution of the group is tracked and two lineages identified, comprising 47 nominal species assigned to 14 genera, 9 of which are new: *Stoyanowella*, *Philippiella*, *Garatella*, *Weaverella*, *Neuquenella*, *Pseudoyaadia*, *Popenoella*, *Louella*, and *Tashiroella*. One lineage (Yaadiinae nov.) migrated northwards from its Tethyan origin into the Cordilleran Province of the Boreal Realm and thence, in the Late Cretaceous, to the Oriental Province, surviving in both biocoenoses into the Maastrichtian. The second lineage, the subfamily Steinmanellinae, appeared in the Early-Middle Kimmeridgian of the American Province, but its centre of diversification was in the Andean Province where it appeared in the Early Tithonian and survived until the Late Hauterivian. From there it migrated eastwards into the Ethiopian Province, reaching as far as India, where it is recorded only from the Late Valanginian and Barremian.

Key words: Bivalvia, Trigoniida, Myophorelloidea, Steinmanellidae, evolution, classification, new taxa.

1. Introduction

Early workers referred all large “knobby trigoniids” to the “section Quadratae” (AGASSIZ 1840; LYCETT 1872), and COX (1952, 1969) assigned them to only two genera, *Steinmanella* and *Yaadia*, thereby “...confounding lineages that can be distinguished over a long period of geological time” (SAUL 1978: 5). STEINMANN (1881, 1882) was the first to appreciate that the Gondwanic representatives were phylogenetically distinct from European Quadratae and introduced the term “Pseudo-Quadratae” for South American *Trigonia transitoria* STEINMANN and South African *T. herzogi* GOLDFUSS, the only two representatives known at that time. Subsequently the concept and range of the group was

extended by the addition of species from the Ethiopian Province, *T. mamillata* KITCHIN (1903) from India, *T. holubi* KITCHIN (1908) from South Africa, and *T. hennigi* LANGE (1914) from East Africa. As a result CRICKMAY (1930) established the genus *Steinmanella*, with *T. holubi* as type, and DIETRICH (1933) introduced *Transitrigonia* for Andean *T. transitoria*. Later, RENNIE (1936) and COX (1952, 1969) synonymized the two genera, SVEL'EV (1958) included *Steinmanella* in the synonymy of *Quadratotrighonia* and POULTON (1977) treated it as a subgenus of *Myophorella*. However, the description of still more species resulted in their resurrection at the subgeneric level (CAMACHO & OLIVERO 1985; H.A. LEANZA 1993) and revealed a far more complex evolutionary history than first envisaged. As a result COOPER

(1991) introduced the subfamily Steinmanellinae for this predominantly Gondwanic group, which includes the largest-known trigoniids, and their Boreal offshoots. However, taxonomic lumping has obfuscated the diversification and complexity of the group and the purpose of this paper, therefore, is to track the evolutionary history of steinmanellids and to represent their diversity in an appropriate taxonomy which replicates genealogy. Again we would reiterate (cf. COOPER 2015) that in phylogenetic taxonomy, taxonomic rank is not discretionary, but it is pre-determined by evolutionary position. Suggestions we have oversplit the group reflect a Linnean approach in which taxonomic limits are subjectively pre-determined, and hence do not accurately replicate genealogy. We stress also that, due to rampant convergence, palaeobiogeographical considerations are fundamental to generic identification (cf. COOPER 1915: 15), as are seemingly “trivial characters”.

This work is dedicated to Dr RENATO REYES-BIANCHI, and to the memory of Dr ERNESTO PERÉZ D'ANGELO, foremost students of the Steinmanellidae.

2. Palaeobiogeography

Steinmanellids are strongly provincial bivalves first recorded from the Early-Middle Kimmeridgian of the American Province (CRAGIN 1897, 1905). However, their centre of diversification is the Andean Province (with 22 nominal species) where they appeared in the Early Tithonian and from where they have been recorded and figured by many workers (STEINMANN 1881, 1882; PHILIPPI 1899; BURCKHARDT 1900a, b, 1903; HAUPT 1907; DOUVILLÉ 1910; LISSON 1930; WEAVER 1931; A.F. LEANZA 1941; LAMBERT 1944; A.F. LEANZA & CASTELLARO 1955; CORVALÁN & PÉREZ 1958; LEVY 1969; REYES & PÉREZ 1978; REYES et al. 1981; PÉREZ et al. 1981; CAMACHO & OLIVERO 1985; H.A. LEANZA & GARATE 1987; LO FORTE 1988; PÉREZ & REYES 1989; H.A. LEANZA 1993; LUCI 2010; LUCI & LAZO 2012; LAZO & LUCI 2013). From here the group migrated eastwards, entering the Ethiopian Province in the Late Valanginian and surviving into the Barremian. Here it is recorded from South Africa (GOLDFUSS 1837; KITCHIN 1908; RENNIE 1936; COOPER 1979, 1991), East Africa (LANGE 1914) and India (KITCHIN 1903; RUDRA et al. 2007). A second group penetrated the Cordilleran Province in the Middle Valanginian where it persisted into the Maastrichtian (GABB 1864, 1876; WHITEAVES 1879; PACKARD 1921; CRICKMAY 1930; ANDERSON 1938,

1958; POULTON 1977; SAUL 1978, 1991; SCOTT 2007). From there steinmanellids migrated westwards, reaching the Oriental Province in the Cenomanian where, again, they persisted into the Maastrichtian (YEHARA 1923a, b; KUBOTA 1955; KOBAYASHI & AMANO 1955; NAKANO 1958, 1961; HAYAMI 1975; TASHIRO 1978, 1988, 1992; MOROZUMI et al. 1981; TASHIRO & MOROZUMI 1983; TASHIRO & KANO 1989). The group was extinct before the end of the Maastrichtian in both the Cordilleran and Oriental provinces.

Palaeomagnetic data (KENT & IRVING 2010) indicate that North America underwent mainly northward drift throughout the Jurassic and Cretaceous, with the Gulf of Mexico positioned at 15° N of latitude in the Late Jurassic (160 Ma) and at about 22° N in the Early Cretaceous (120 Ma). This suggests that Kimmeridgian-Tithonian *Stoyanowella* n.g. lived in subtropical to warm temperate waters on the Tropic of Cancer, between 35–40° N of latitude. Early Cretaceous North American yaadiines inhabited temperate waters between 45–60° N of latitudes, suggesting adaptation to somewhat cooler waters (Fig. 1). As the southern tip of the Yucatán Peninsula was positioned on the Tropic of Capricorn at 30° S of latitude at the beginning of the Jurassic 220 Ma ago, much of the Gondwanic Realm experienced cool temperate and subpolar conditions for most of the Jurassic and Cretaceous. Obviously northward drift of Gondwana during the Late Cretaceous would have seen progressive warming of water conditions during this period.

Steinmanellids have a bipolar distribution, Yaadiinae nov. favouring cool temperate waters in the Boreal Realm (cf. COOPER 2015 for trigoniid palaeobiogeographical map) and Steinmanellinae inhabiting similar waters in the Gondwanic Realm. However, whereas the former preferred high-energy nearshore environments with coarse-clastic sediments (SAUL 1978), the latter favoured low-energy sticky-clay facies of lagoonal and back-barrier origin (LAZO 2003; pers. observ.). The family avoided tropical warm-water ecosystems dominated by reef-building corals, calcareous algae, microbial bioherms, orbitoline foraminifers and rudistid bivalves. Undoubtedly, their absence from southern and eastern Gondwana, i.e. the Antarctic and Maorian provinces, is also environmentally induced, to avoid very cold circum-polar waters. Conditions in the Australasian Province were also detrimental to steinmanellids, but the precise reasons unknown.

Nominal species referred to Steinmanellidae from the different faunal provinces used here (see COOPER 2015: 14, fig. 1) are as follows:

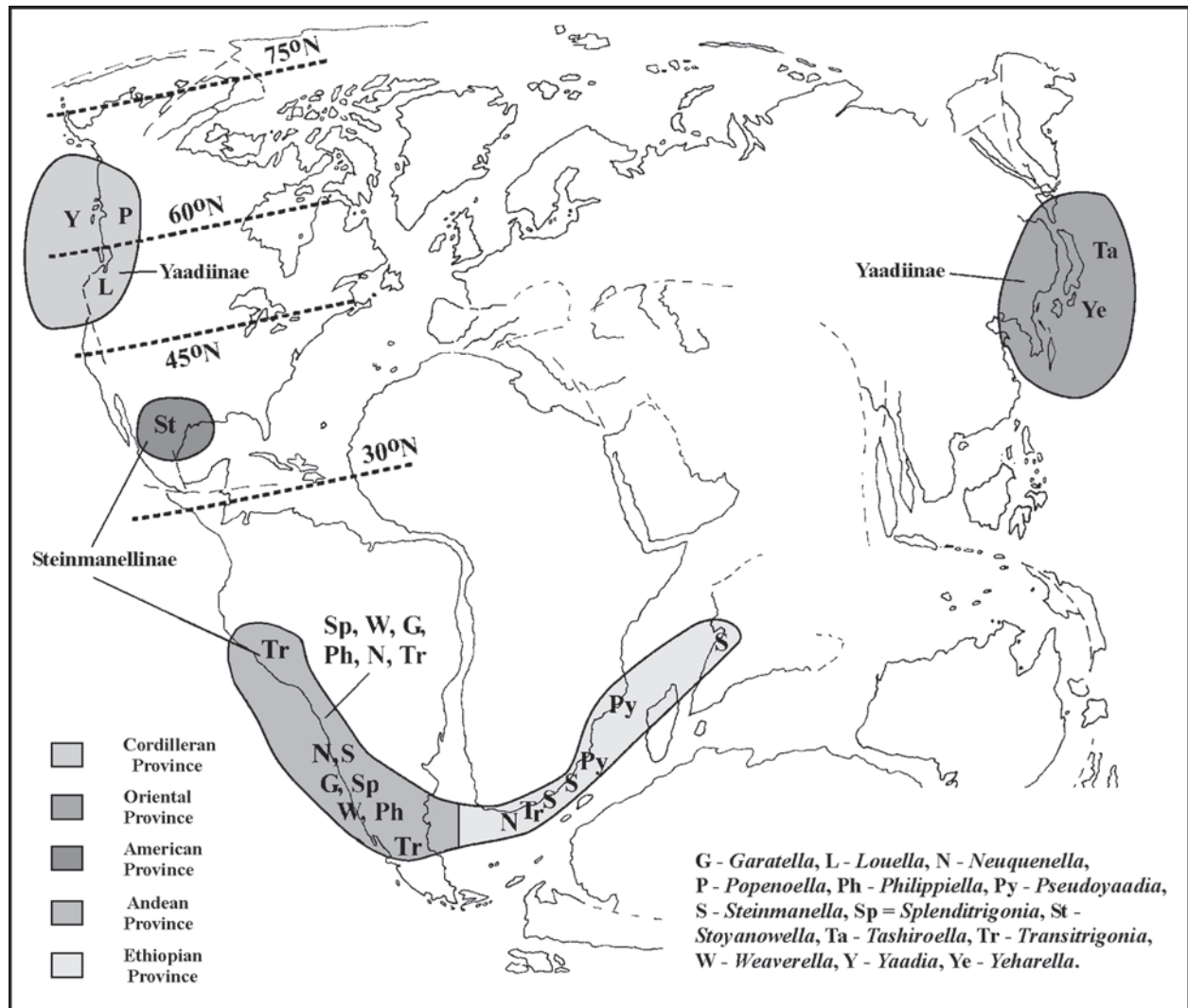


Fig. 1. The palaeobiogeographical distribution of steinmanellid bivalves (Hauterivian continental reconstruction after OWEN 1983). Trigoniid palaeobiogeographical provinces are after COOPER (2015). The lines of latitude are for the Barremian (120 Ma) taken from KENT & IRVING (2010).

Oriental Province

ainuana YABE & NAGAO, *deckeina* KABOTA, *japonica* YEHARA, *jimboi* KOBAYASHI & AMANO, *kimurai* TOKUNUGA & SHIMIZU, *lymani* KOBAYASHI & AMANO, *obsoleta* KOBAYASHI & AMANO, *sanukiensis* NAKANO, *shinoharai* KOBAYASHI & AMANO, *tanii* TASHIRO & MOROZUMI.

Cordilleran Province

brandti SAUL, *californiana* PACKARD, *colusaensis* ANDERSON, *fitchi* PACKARD, *hemphilli* ANDERSON, *jonesi* SAUL, *leana* GABB, *lewisagassizi* CRICKMAY, *perrinsmithi* ANDERSON, *pineae* SAUL, *robusta* SAUL, *wheelerensis* ANDERSON, *whiteavesi* PACKARD.

American Province

maloneana STOYANOW, *sologureni* FELIX, *vyschetskii* CRAGIN.

Andean Province

caicayensis LAZO & LUCI, *erycina* PHILIPPI, *haupti* LAMBERT, *herzogi* REYES (non GOLDFUSS), *katterfeldensis* CAMACHO & OLIVERO, *lepida* PHILIPPI, *neuquensis* BURCKHARDT, *pehuenmapuensis* H.A. LEANZA, *posadensis* CAMACHO & OLIVERO, *quintucoensis* WEAVER, *raimondii* LISSON, *splendida* A.F. LEANZA, *steinmanni* PHILIPPI, *subquadrata* LUCI & LAZO, *transitoria* STEINMANN, *vacaensis* WEAVER.

Ethiopian Province

hennigi LANGE, *herzogi* GOLDFUSS, *holubi* KITCHIN, *kensleyi* COOPER, *mamillata* KITCHIN.

With regard to the Andean Province, Tithonian *Trigonia copiapina* PHILIPPI (1899: 71, pl. 32, fig. 1; PÉREZ & REYES 1989: 22), *T. stolpi* PHILIPPI (1899: 81, pl. 35, fig. 6; PÉREZ & REYES 1989: 17) and *T. erycina* var. *irregularis* PHILIPPI (1899: 66, pl. 32, fig. 3) are based on generically-indeterminate internal moulds whose type specimens are lost (PÉREZ & REYES 1989). The holotype of Neocomian *T. williamsi* PHILIPPI (1899: 72, pl. 32, fig. 4; PÉREZ & REYES 1989: 24) is also lost and its curious shape with prominent umbones is not a feature of steinmanellines; it may be teratological. *Trigonia clavellata* PHILIPPI (*non* PARKINSON) 1899: 63, pl. 29, figs. 3, 4) was assigned to *Steinmanella* by PÉREZ & REYES (1989: 9, pl. 1, fig. 15) but the species was based upon two fragments both of which do not preserve the ornament of the area or escutcheon and hence are generically indeterminate. Moreover, the Aptian age of the material suggests it may be myophorelline. Here all these species are regarded as *nomina dubia* and are not discussed further.

Trigonia amarali PHILIPPI (1899: 67, pl. 30, fig. 6; PÉREZ & REYES 1989: 22) (Fig. 4J) is based on a medium-sized (L = 57 mm), moderately inequilateral, Tithonian specimen with a pyriform shape, strongly-rounded anterior with umbones positioned well back, and prominent transverse costellae to the escutcheon. Its shape is unlike that of any steinmanelline and it appears closer to Japanese material currently assigned to *Heterotrigonia*. We do not regard it a steinmanelline.

3. Systematic palaeontology

Repositories of material referred to here are as follows: BMNH – Natural History Museum, London; DNSM – Natural Science Museum, Durban; MOZ – Museo Juan

Olsacher, Zapala; SAM – South African Museum, Cape Town; MLP – Museo de La Plata; UO – Condon Museum, University of Oregon, Eugene; USNMNH – Smithsonian Institute, Washington.

Superfamily Myophorelloidea KOBAYASHI, 1954

Family Steinmanellidae COOPER, 1991

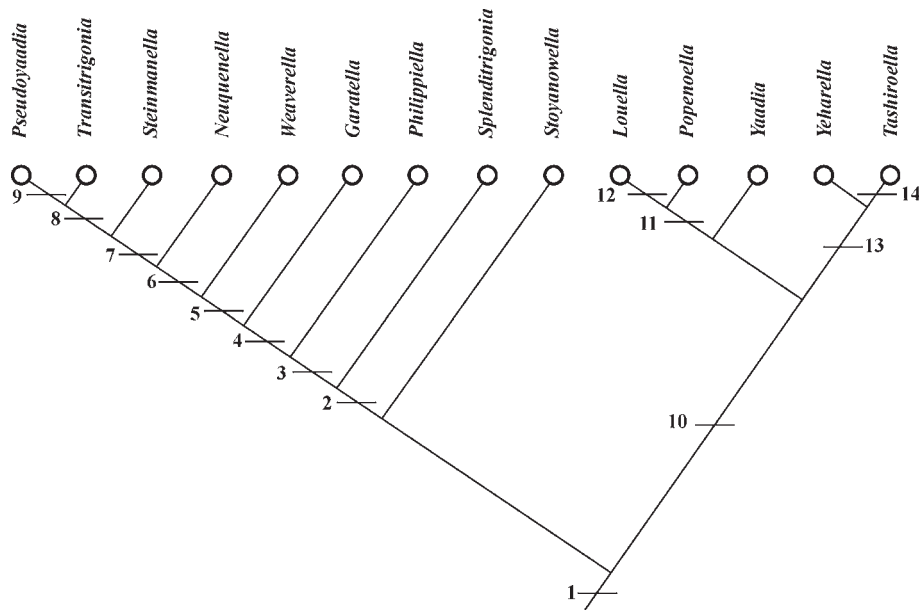
(nom. transl. herein ex Steinmanellinae)

Diagnosis: Moderately large to very large, thick-shelled, strongly inequilateral, moderately inflated, subquadratic to rectangular and subovate with obliquely subtruncate respiratory margin, low subterminal umbones, moderately-incurved opisthogyrus beaks and relatively large ligament nymph; anterior face commonly flat, either unornamented or with upward-concave extensions of flank costae and narrow lunule; escutcheon moderately wide, with commarginal or transverse rows of nodes; broad, flat, generally bipartite area with nodate inner, median and marginal carinae in early to middle growth; area with commarginal costellae continuous from flank in earliest growth but in middle growth with growth striae which may persist to maturity (Yaadiinae nov.) or give way to strong irregular commarginal rugae (Steinmanellinae); antecarinal sulcus narrow in early growth, obsolete later when areal rugae commonly extend onto posterodorsal flank; flanks with oblique, curved to almost straight, nodate costae, generally narrower than interspaces, with large subcircular to elliptical nodes which may become drawn out and attenuated ventrally; LV with weak lath-like anterior tooth. *Early-Late Kimmeridgian – Maastrichtian*.

Discussion: As recognized by STEINMANN (1882), and many subsequent workers, the similarity of steinmanellids to Quadratotrioniinae is convergent. In the latter there are V-shaped flank costae in early growth, the longitudinal furrow to the area is closer to the marginal than to the inner carina, and internally there are pits to the posteroventral commissure (KITCHIN 1903).

The early growth stages of steinmanellids, with nodate carinae and curved rows of flank nodes, point indubitably to an origin in Jurassic Myophorellidae (STEINMANN 1882; KITCHIN 1908; RENNIE 1936; KOBAYASHI & AMANO 1955; SAVEL'EV 1958; NAKANO 1968; REYES et al. 1981; COOPER

Fig. 2. Hypothesized relationships among Steinmanellidae. It is important to appreciate that the phenotypic discontinuities represented by the gaps between adjacent branches of the cladogram are inherently unequal and hence an indication only of affiliation among known members and not necessarily a very close evolutionary relationship. **1.** Moderately large, thick-shelled, elongate-ovate, moderately inflated, low subterminal umbones, moderately-incurved opisthogyrus beaks, relatively large ligament nymph; gently-convex anterior margin, long convex ventral margin, obliquely subtruncate respiratory margin, long almost straight posterodorsal margin; escutcheon moderately wide, with transverse rows of nodes; narrow flattened anterior face with fine rib extensions; bipartite area with nodate inner, median and marginal carinae, median carina weaker than others; area beaded in early growth, later with irregular growth rugae which may extend onto posterodorsal flank; marginal carina nodate, nodes increasing in size posteriorly; antecarinal sulcus lacking; flanks with gently curved nodate



costae with opisthoclinal dorsal stems. **2.** Subquadratic; anterior margin subvertical, almost straight, posterodorsal margin short; escutcheon large, with transverse rows of enlarged nodes; entire area nodate. **3.** Elongate-subovate; escutcheon with commarginal (oblique) rows of beads; escutcheon carina with enlarged nodes becoming increasingly elongate posteriorly. **4.** Area non-tuberculate, with irregular growth rugae in middle to later growth; nodate median carina obsolete in later growth; ribs strongly curved, with relatively-small nodes. **5.** Elongate-ovate, with convex anterior margin; flank costae without dorsal stems, terminating mostly along anterior margin, becoming subtransverse to ventral margin in later growth, flank nodes decreasing in size and becoming increasingly crowded posteriorly. **6.** Moderately large to large, subtrigonal, with straight, vertical anterior margin, ribbed anterior face; relatively short, straight posterodorsal margin; flank costae strongly curved, mostly intersecting anterior margin, sometimes with gaps and enlarged and irregular nodes on anterolateral shoulders. **7.** Large to very large, subrectangular, with subparallel ventral and posterodorsal margins; narrow unornamented anterior face; narrow antecarinal space in early to middle growth, becoming obsolete later with encroachment of growth rugae from area; flank costae with nodes increasing in size posteriorly and becoming irregular anterolaterally, with gaps and occasional larger tubercles. **8.** Very large, massive, very elongate-ovate to subrectangular; anterior margin inclined, with acute umbonal angle; ligament nymph relatively small; flank costae straight, relatively distant, posteriorly opisthoclinal, mostly terminating along ventral margin, nodes increasing in size posteriorly; escutcheon with transverse or commarginal costellae. **9.** Ovate-elongate; escutcheon relatively broad, in early growth with transverse nodate costae, nodes becoming oblique in middle growth and hence commarginal; in earliest growth area with commarginal costellae; nodate median and marginal carinae obsolete in middle to later growth when area ornamented by growth striae only; curved flank costae narrower than interspaces, about half terminating on anterolateral shoulder in disconnected double row of enlarged tubercles. **10.** Moderately large; anterolateral corner subangular; escutcheon subtabulate, with transverse rows of nodes; inner carina with strong transverse bars which in early growth extend across inner area to reach longitudinal furrow; area with fine diagonal (commarginal) costellae on outer part; narrow unornamented antecarinal space; flanks with 1-2 vertical rows of enlarged tubercles on anterolateral shoulders more-or-less separated from weakly-curved, oblique flank costae with large nodes. **11.** Anterior margin convex, with rounded anterolateral corner, round anterolateral shoulders lacking enlarged tubercles and convex anterior face; umbones positioned back from anterior, posterodorsal margin concave; narrow shallowly-sunken escutcheon smooth or with strong subtransverse costellae continuous from area; very-large ligament nymph; juvenile ribbing of area may form complicated chevrons; nodate marginal carinae evanescent in later growth. **12.** Elongate-subovate, with fastigiate anterior face; posterodorsal margin almost straight; escutcheon large, in early growth with bar-like transverse costae, later unornamented and poorly discriminated from area, fastigiate on conjoined valves; inner carina non-tuberculate, marked only by a change in slope; area broad, gently convex, with fine oblique costellae and longitudinal groove in early growth only; curved flank costae numerous, broader than interspaces, with small uniform nodes, in later growth cutting obliquely across growth striae anteriorly, forming zigzags anteroventrally. **13.** Subquadratic to subovate; escutcheon with oblique costellae meeting commissure in posteriorly-directed chevrons; nodate inner, median and marginal carinae evanescent in later growth; area with commarginal costellae in earliest growth, later with growth striae only; strongly-curved nodate flank costae, narrower than interspaces, most terminating along anterior margin, nodes tending to elongate and coalesce in later growth to become segmented subcommarginal cords. **14.** Very narrow, short, unornamented escutcheon; nodate inner, median and marginal carinae restricted to early growth (primitive) or obsolete (derived); broad bipartite area unornamented; nodate flank costae evanescent posteriorly in middle to later growth leaving flanks with growth striae only.

1991), from which they differ most obviously in their larger size, robust shell and ornamented escutcheon. NAKANO (1968) looked to *Orthogonia* for the progenitor of *Yaadia*, whereas SAUL (1978) favoured myophorellines with enlarged shoulder tubercles, i.e. *Scaphogonia* and *Scaphotrigonia*. However, this latter character has occurred repeatedly in myophorellid evolution and is highly convergent (cf. COOPER 2011), and the precise antecedent of steinmanellids remains unknown since they are separated by a moderate phenotypic discontinuity from other myophorellids. Hypothesized relationships among the steinmanellid genera recognized here are shown as Fig. 2.

Subfamily Steinmanellinae COOPER, 1991

Diagnosis: Moderately large to very large; escutcheon nodate, either in transverse (primitive) or commarginal (derived) rows; area primitively nodate or not, later with coarse, irregular, commarginal rugae in middle to later growth, commonly extending onto posterodorsal flank with obsolescence of marginal carina. *Early-Late Kimmeridgian – Barremian*.

Discussion: Steinmanelline bivalves are characteristic of Western Gondwana (Andean and Ethiopian provinces) (CAMACHO & OLIVERO 1985; COOPER 1991; H.A. LEANZA 1993). Their diversity has long been recognized and, following multivariate analysis, REYES et al. (1981) distinguished 3 major groups: the (A) *transitoria*, (B) *erycina* and (C) *steinmanni* groups, with *S. splendida* remaining isolated but with strong affinities with the *transitoria* group.

Within the *transitoria* group (A), REYES et al. (1981) distinguished 3 subgroups, A₁ comprising *transitoria*, *curacoensis*, *quintucoensis* and *herzogi*, A₂ made up of *vacaensis*, and A₃ with *neuquensis* and *raimondii*. Within the *erycina* group (B) they recognized two subgroups, B₁ made up of *erycina* and *haupti*, and B₂ consisting only of *neuquensis* (excluding the forms described by WEAVER and LAMBERT) which was considered intermediate between the *erycina* and *transitoria* groups. The *steinmanni* group (C) consisted only of the nominate species. Subsequently a number of subgenera were introduced to encompass this variation (cf. CAMACHO & OLIVERO 1985; H.A. LEANZA 1993), but these taxa have failed to gain acceptance on the grounds they were "... rather poorly defined" (LUCI & LAZO 2012: 104). Here we provide new diagnoses.

Genus *Stoyanowella* nov.

Etymology: For Dr. ALEXANDER A. STOYANOW (1879–1974), monographer of the Early Cretaceous faunas of southeastern Arizona (cf. LEE & SCHROTER 1977).

Type species: *Trigonia vyschetszkii* CRAGIN, 1893; by original designation herein.

Stoyanowella vyschetszkii (CRAGIN, 1893) Fig. 3A, B

Diagnosis of genus: Moderately large, subovate, longer than high with near-terminal umbones and gently-convex anterior margin curving evenly into long convex ventral margin; respiratory margin obliquely subtruncate and long posterodorsal margin almost straight; escutcheon broad, with nodate transverse costellae; narrow flattened anterior face with fine ribs; bipartite area with nodate inner, median and marginal carinae, median row weaker than others and nodes of marginal carina increasing in size posteriorly and becoming more elongate; in early growth area with commarginal rows of beads which, in middle to later growth, coalesce to produce irregular growth rugae which may extend onto the posterodorsal flank; marginal carina nodate, nodes increasing in size posteriorly, extending onto outer flank; antecarinal sulcus lacking; flanks with gently curved nodate costae, nodes rounded to elliptical, increasing in size posteriorly, often with single very large node near ventral margin; flank costae with thin, finely tuberculate, opisthoclinal dorsal stems. *Early-Late Kimmeridgian*.

Referred species: *S. maloneana* (STOYANOW 1949: 72 (*pars*), pl. 9, figs. 1–2 only) (Fig. 3C, D).

Discussion: *Stoyanowella* n.g. is endemic to the American Province (Texas). As the oldest member of the Pseudo-Quadratae, and the only non-Gondwanic representative, *S. vyschetszkii* has a critical bearing on the origin of the family. CRAGIN (1893) introduced the species for material from the Malone Formation of Texas. These trigoniids occur in the lower part of the formation which was dated on the basis of the associated ammonites to the Early-Middle Kimmeridgian (ALBRITTON 1937; IMLAY 1980). However,

Fig. 3. A, B – *Stoyanowella vyschetszkii* (CRAGIN), lectotype (A) and paralectotype (B), after CRAGIN (1905). **C, D** – *Stoyanowella maloneana* (STOYANOW), the holotype after SCOTT (2007). **E–F, L, M** – *Philippiella erycina* (PHILIPPI). E–F, a hypotype figured by WEAVER (1931); L, the lost syntype for which the species was created, after PHILIPPI (1899); M, the lectotype selected by PÉREZ & REYES (1989). **G, H** – *Splenditrigonia splendida* (A.F. LEANZA), the holotype, MLP-4128. **I, V** – *Philippiella haupti* (LAMBERT); I, a topotype after H.A. LEANZA (1993); V, the lectotype after LAMBERT (1944). **J, K** – “*Trigonia*” *sologureni* FELIX, the holotype by monotypy, after FELIX (1891). **N** – “*Trigonia*” *volckmanni* PHILIPPI, the holotype after PÉREZ & REYES (1989). **O–Q** – *Garatella quintucoensis* (WEAVER), the lectotype designated herein, after LUCI & LAZO (2012). **R** – *Garatella neuquensis* (BURCKHARDT), the holotype, after LUCI & LAZO (2012). **S, T** – *Garatella subquadrata* (LUCI & LAZO), the holotype after LUCI & LAZO (2012). **U** – *Garatella raimondii* (LISSON), the holotype, after LISSON (1930).

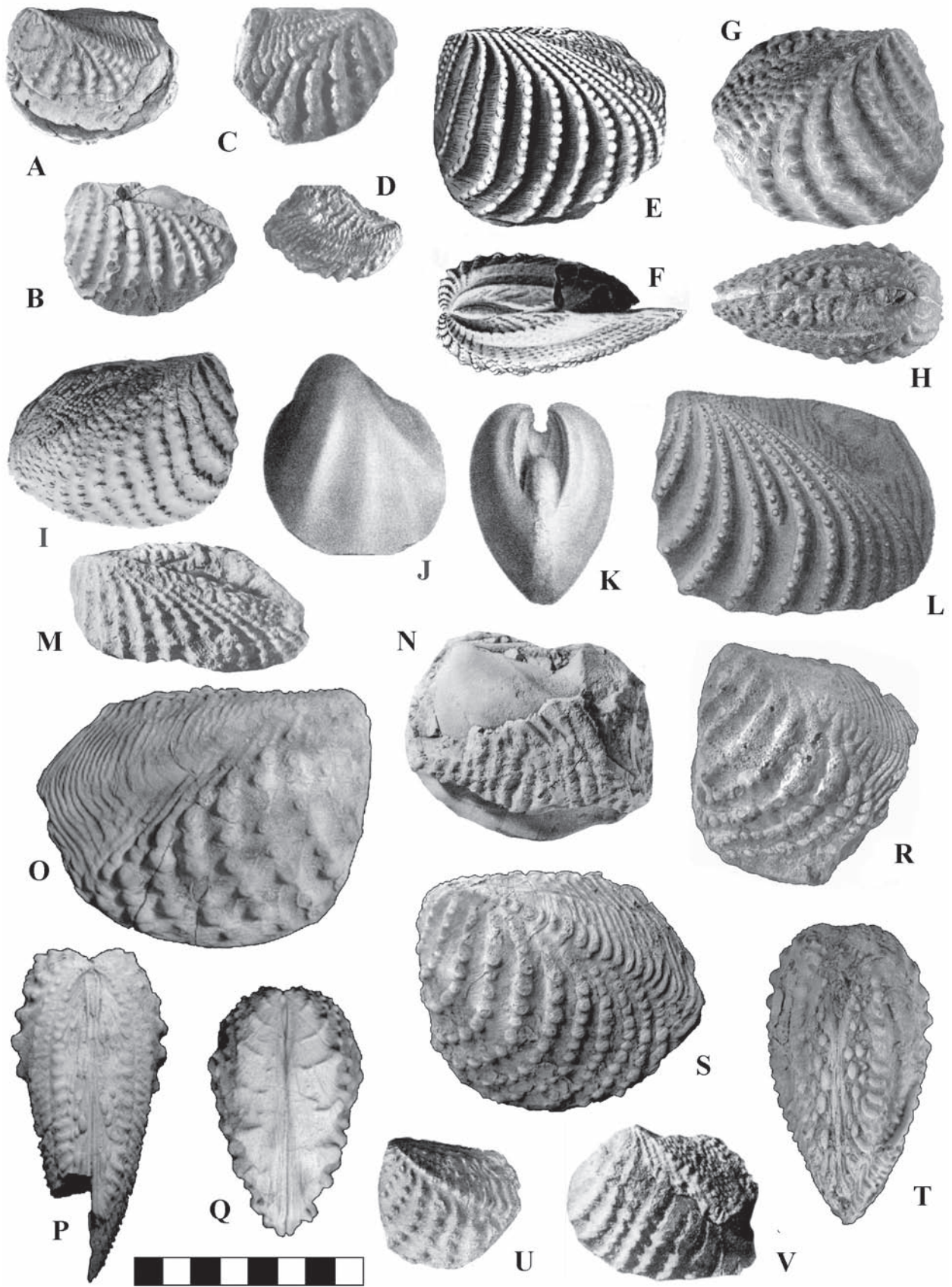


Fig. 3.

it was only later (CRAGIN 1905: 56, pl. 8, figs. 1-2, pl. 9, figs. 1-3) that the species was described in detail and figured for the first time. CRAGIN recognized that the absence internally of commissural pits precluded assignment to *Quadratotrigonina* and considered *T. vyschetskii* related to *T. transitoria*, while acknowledging that none "... has the condition of *Trigonina transitoria* STEINMANN in which the untuberculated median carina is barely indicated, whereas the solid costellae are strongly sculptured in the posterior part of the areas". STOYANOW (1949) referred *T. vyschetskii* to the Pseudo-Quadratatae, and NAKANO (1961), SAUL (1978) and SCOTT (2007) assigned it to the genus *Steinmanella* without discussion.

STOYANOW (1949: 72) restudied CRAGIN's type material and suggested that at least 3 species were involved. His determinations were as follows:

pl. 8, fig. 1, pl. 9, fig. 3 – *Trigonina* sp. (USNMNH-28967).

pl. 8, fig. 2 – lectotype of *Trigonina vyschetskii* (USNMNH-28967) (Fig. 2A).

pl. 9, fig. 1 – holotype of *Trigonina maloneana* STOYANOW (USNMNH-92020) (Fig. 3C, D).

pl. 9, fig. 2 – *T. maloneana* var. (USNMNH-28967).

This assessment was refuted by SAUL (1978) and SCOTT (2007) both of whom, without in-depth analysis, admitted only one species. However, there are differences; *S. maloneana* lacks opisthocline stems to its flank costae and a flattened anterior face (cf. CRAGIN 1905, pl. 9, fig. 2), and has coarser flank tubercles. Moreover, SCOTT (2007) considered *Trigonina vyschetskii* most similar to Late Aptian *T. guildi* STOYANOW (1949: 75, pl. 12, figs. 1-2) but the latter is clearly a member of the *Quadratotrigoninae*, with V-shaped flank costae in early growth. Given its abundance, and the critical position of *Stoyanowella* n.g. in steinmanellid phylogeny and, indeed, its significance to the suggested monophyly of the group, the Malone material warrants further collecting and thorough re-analysis, especially since *S. vyschetskii* "... was found by scores, in one or two places being agglomerated in beds, mingled more or less with other fossils. Between 75 and 100 specimens of it are represented from this tract. But if the shells of other Malone fossils, as here preserved, prove fragile under the rigorous temperature changes of a plateau climate, that of *Trigonina vyschetskii* is so especially, and of the large number collected many are in half-released fragments, and comparatively few make even tolerably fair cabinet specimens" (CRAGIN 1905: 57).

CRAGIN (1905: 57) suggested that *Trigonina sologureni* FELIX (1891: 179, pl. 27, fig. 2) "approached" some specimens of *S. vyschetskii*. However, the Mexican species is based on an internal mould (Fig. 3J, K) which is shorter, more inflated and subquadratic and, without more information, is generically unidentifiable. It is a *nomen dubium*.

At present there is no known ancestor for *Stoyanowella* n.g. Unfortunately the genus *Myophorella* as currently interpreted (COX 1969) is a sac-name for a number of generically-distinct clades, i.e. a taxonomic mess, and hence comparison with steinmanellines virtually impossible. Certainly there is a high degree of convergence among the two groups, e.g. "*Trigonina keepingi* LYCETT (1877: 196, pl. 35, figs. 1, 2). Among potential myophorelline candidates, Tethyan *Trigonina clavellata* (J. SOWERBY, 1815) (LYCETT 1872: 18, pl. 1, figs. 1, 2), a junior homonym of *T. clavellata* PARKINSON

(1811), comes closest, being moderately large and similarly robust, with 3 well-developed nodate carinae, but its elongate-ovate shape, unornamented escutcheon, lack of growth rugae to the area and absence of opisthocline dorsal stems to the flank costae immediately distinguish it. However, according to CHAMBERLAIN's comments of the ETHELDRED BENETT (1831) collection (cited by TORRENS et al. 2000: 110), the forms of *T. clavellata* from the Oxford Clay "... involve a much greater amount of differences than that which in other forms of the genus is regarded as of specific importance". Thus, without taxonomic revision, *T. clavellata* is also almost impossible to interpret; S. SCHNEIDER (in litt.) regards it a junior subjective synonym of *T. nodulosa* BAYLE. *Promyophorella* has a similarly wide area to *Stoyanowella* n.g. but is much smaller and thin-shelled, with an unornamented escutcheon, fine commarginal lirae to the area and it lacks a beaded median carina.

Since *Stoyanowella* n.g. is separated from all known myophorellines by a moderate phenotypic discontinuity here the subfamily Steinmanellinae is elevated to family rank.

Genus *Splenditrigonia* H.A. LEANZA, 1993

Type species: *Trigonina splendida* A.F. LEANZA 1941: 225, pl. 1, figs. 1, 2; by original designation.

Splenditrigonia splendida (A.F. LEANZA, 1941) Fig. 3G, H

Diagnosis of genus: Like *Stoyanowella* n.g. but subquadratic; escutcheon large, wide, with subtransverse rows of enlarged nodes; broad bipartite area with rows of small nodes in both subcommarginal and diagonal rows which persist to maturity; nodate median and marginal carinae obsolete in middle to later growth; antecarinal sulcus lacking; posterior flank costae with short opisthocline dorsal stems meeting marginal carina at very acute angle. *Early Tithonian*.

Discussion: *Splenditrigonia* is a monotypic Andean endemic (Argentina) introduced as a subgenus of *Steinmanella* but here elevated to generic rank. Its nodate area distinguishes it from all but *Philippiella* n.g. With respect to its origin it is important to recall CRAGIN's (1905: 56) observation that the areal ornamentation of *S. vyschetskii* "... shows considerable mutability, and a variety occurs in which the entire area is covered with small compressed tubercles". This latter variant has neither been figured nor described, nor has it been shown to be conspecific, but it certainly makes *S. vyschetskii* a strong candidate for the origin of *Splenditrigonia*.

COOPER (1991) united Vaugoniinae and Quadratotrigininae as Vaugoniidae on the basis of their V-shaped flank costae in early growth, an inferred apomorphy, with *Quadratotrigonina* separated by its quadratic shape and nodate areal ornament. However, the apparent presence of *Stoyanowella* "variants" with nodate areas raises the possibility that Steinmanellinae and Quadratotrigininae may be sister taxa, and it is the V-shaped flank costae of Vaugoniinae that are convergent. Clearly better knowledge of the Malone fauna is critical to unraveling this quandary.

Genus *Philippiella* nov.

Etymology: In memory of Dr. RODOLFO AMANDO PHILIPPI (1808-1904), University of Chile, monographer of the Jurassic-Cretaceous bivalves of Chile.

Type species: *Trigonia erycina* PHILIPPI 1899: 66, pl. 30, figs. 3, 5; WEAVER 1931: 259, pl. 21, figs. 109-110; LAMBERT 1944: 379, pl. 8, fig. 4; REYES et al. 1981: 38, pl. 2, figs. 3-8; PÉREZ & REYES 1989: 9, pl. 1, figs. 5, 10; H.A. LEANZA 1993: 44, pl. 7, fig. 1; by original designation herein.

Philippiella erycina (PHILIPPI, 1899)

Fig. 3E, F, L

Diagnosis of genus: Like *Splenditrigonia* but subrectangular to elongate-subovate, longer than high, with commarginal rows of beads to the escutcheon, and small nodes to the area; flank costae terminate mostly along the ventral margin, with relatively long, opisthocline dorsal stems and smaller nodes. *Late Tithonian*.

Referred species: *P. haupti* (LAMBERT 1944: 381, pl. 5, fig. 7; H.A. LEANZA 1993: 44, pl. 6, figs. 1, 2) (Fig. 3I).

Discussion: *Philippiella* n.g. is endemic to the Andean Province (Chile, Argentina) and comprises two closely-related Late Tithonian (*Corongoceras alternans* Zone) species (H.A. LEANZA 1993). The genus corresponds to the B₁ group of REYES et al. (1981) which is morphometrically well separated from ancestral *S. splendida*, with derived characters placing it closer to *Garatella* n.g.

Trigonia erycina was based upon an almost-complete specimen (PHILIPPI 1899, pl. 30, fig. 3) (Fig. 3L) which appears to have been lost. As a result PÉREZ & REYES (1989: 9) selected the second imperfect syntype (pl. 1, fig. 5), identified as *T. erycina* var., as lectotype. *Trigonia erycina* var. *irregularis* PHILIPPI (1899: 66, pl. 32, fig. 3; PÉREZ & REYES 1989: 22) and *T. volckmanni* (PHILIPPI 1899: 72, pl. 32, fig. 5; PÉREZ & REYES 1989: 10, pl. 2, figs. 17, 18) (Fig. 3N), are based on poorly-preserved specimens and both have been included in the synonymy of *P. erycina*.

Genus *Garatella* nov.

Etymology: For the late Dr. JOSÉ I. GARATE ZUBILLAGA (Zapala), in recognition of his contribution to the knowledge of trigoniids in the Neuquén Basin of Argentina.

Type species: *Trigonia quintucoensis* WEAVER (1931: 248, pl. 21, fig. 111, pl. 23, figs. 119-125; BMNH-C.119 is selected here as lectotype; by original designation.

Garatella quintucoensis (WEAVER, 1931)

Fig. 3O-Q

Diagnosis of genus: Like *Philippiella* n.g. but larger (Lmax = 120 mm), subquadratic, almost as high as long, with sub-

terminal umbones, straight subvertical anterior margin and rounded anteroventral corner; escutcheon carina persistent, nodes becoming increasingly elongate with growth; non-tuberculate area with irregular growth rugae which, in middle to later growth, absorb the nodate marginal carina and extend well onto the flank, displaying a prominent furrow below the marginal carina posteriorly expanded; flank costae strongly curved, terminating mostly along the anterior and anteroventral margins. *Late Berriasian* – *Early Valanginian*.

Referred species: *G. neuquensis* (BURCKHARDT 1903: 74, pl. 14, figs. 4-6); LAZO & LUCI 2013: 113, fig. 11) (Fig. 3R), *G. raimondii* (LISSON 1930: 15, pl. 8, figs. 1-2) (Fig. 3U), *G. subquadrata* (LUCI & LAZO 2012: 110, figs. 9, 10; = *T. neuquensis* WEAVER (non BURCKHARDT) 1931: 253, pl. 22, figs. 112-114) (Fig. 3S).

Discussion: *Garatella* n.g. is endemic to the Andean Province (Argentina, Peru). It corresponds to the A3 group of REYES et al. (1981) and is easily distinguished from *Philippiella* n.g., to which it is morphometrically closest (cf. REYES et al. 1981), and *Splenditrigonia* by the lack of nodes to the area. *Garatella quintucoensis* retains long, thin, opisthocline, dorsal stems to the flank costae not seen in the other referred species, but a feature of *Philippiella* n.g., and is assumed to be the most primitive member of the group. The apomorphic characters of *Garatella* n.g. foreshadow *Weaverella* n.g.

Contrary to LUCI & LAZO (2012), the holotype of *G. neuquensis* (Fig. 3R) is not an “anterior fragment”. That the areal growth rugae extend well onto the posterodorsal flank shows that it is an almost complete specimen, albeit somewhat corroded, with a broad antecarinal space crossed by growth rugae from the area.

Peruvian *S. raimondii* (Fig. 3U) is based on material <36 mm in length and may be juvenile, as a result of which its status has been questioned. Contrary to LAZO (2003), however, the name is legitimate and nomenclaturally available since it was correctly introduced. Moreover, the type locality is geographically well separated from other steinmanellines, and the species may well prove valid. Topotypic material is required.

Genus *Weaverella* nov.

Etymology: For Dr CHARLES EDWIN WEAVER (1880-1958) (cf. LAZO 2009), whose seminal work on the Jurassic-Cretaceous palaeontology and stratigraphy of west-central Argentina has formed the starting point for much subsequent research.

Type species: *Trigonia transitoria* var. *curacoensis* WEAVER 1931: 243, pl. 22, figs. 115-118; LUCI & LAZO 2012: 104, figs. 5, 6; LAZO & LUCI 2013: 70, fig. 5); by original designation herein.

Weaverella curacoensis (WEAVER, 1931)

Fig. 4A-C

Diagnosis of genus: Elongate-subovate, posteriorly produced, with well-rounded anteroventral margin; ligament

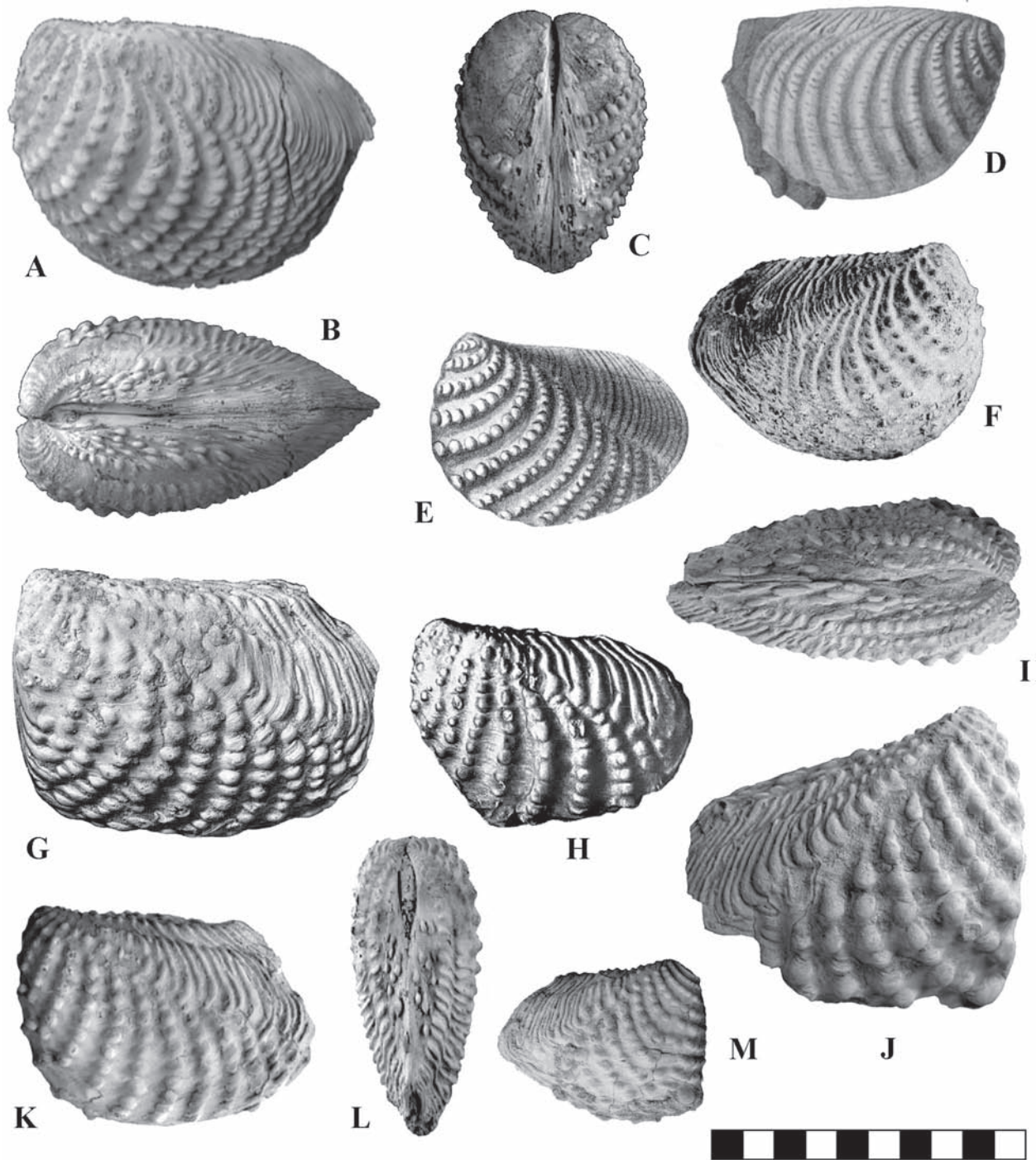


Fig. 4. **A-C** – *Weaverella curacoensis* (WEAVER), the lectotype designated herein, BMNH-C.119, after LUCI & LAZO (2012, fig. 8. 1-3). **D** – *Weaverella lepida* (PHILIPPI), the holotype by monotypy, after PHILIPPI (1899). **E, F** – *Weaverella steinmanni* (PHILIPPI); **E**, the holotype by monotypy, after PHILIPPI (1899); **F**, the neotype selected herein, MOZ P-0917, after H.A. LEANZA & GARATE (1987). **G** – *Steinmanella holubi* (KITCHIN), a topotype figured by COOPER (1991). **H** – *Steinmanella mamillata* (KITCHIN), the lectotype designated herein after KITCHIN (1903). **I, J** – *Neuquenella pehuenmapuensis* (H.A. LEANZA), a topotype after LUCI & LAZO (2012). **K, L** – *Steinmanella caicayensis* LUCI & LAZO, the holotype, after LUCI & LAZO (2012). **M** – *Neuquenella kensleyi* (COOPER), an unnumbered adult topotype in the DNSM.

nymph relatively large; escutcheon with commarginal rows of ellipsoidal nodes replaced by growth rugae and striae in middle to later growth; escutcheon carina with enlarged nodes becoming increasing elongate posteriorly, evanescent in maturity; area with weak, nodate, median and marginal carinae, small and weak nodes transversely elongate in middle growth, becoming obsolete later when growth rugae from area extend onto posterodorsal flank; antecarinal sulcus in early growth only, later obsolete; flank costae strongly curved, terminating mostly along anterior margin with concave-upward extensions on anterior face, becoming subtangential to ventral margin in later growth, meeting area at acute angle; tubercles to flank costae relatively small, decreasing in size and becoming increasingly crowded posteriorly. *Early Valanginian* – *Early Hauterivian*, ?*Barremian*.

Referred species: *W. lepida* (PHILIPPI 1899: 67, pl. 30, fig. 4; PÉREZ & REYES 1989: 10, pl. 1, fig. 11) (Fig. 3D), *W. steinmanni* (PHILIPPI 1899: 64, pl. 30, figs. 1, 2; H.A. LEANZA & GARATE 1987: 216, pl. 13, figs. 1, 2; H.A. LEANZA 1993: 42, pl. 13, figs. 1, 10; non LISSON 1930: 6, pl. 2, figs. 1-3) (Fig. 4E-F)

Discussion: *Weaverella* n.g. is endemic to the Andean Province (Chile, Argentina), corresponding to the A₂ and C groups of REYES et al. (1981). It differs most obviously from *Garatella* n.g. in its elongate-subovate shape, long posterodorsal margin, well-rounded anteroventral corner, strongly-convex ventral margin, areal rugae not passing substantially onto the flank, lack of dorsal stems to the flank costae and smaller flank tubercles.

Although included in the synonymy of *W. curacoensis* by H.A. LEANZA (1993), *W. steinmanni* (Fig. 4E-F) differs in its earlier loss of median and marginal carinae, the smaller nodes to its flank costae, and the finer, more-regular rugae to its area. PHILIPPI (1899) gave its imprecise type locality as "... *declivi orientalis Andium chillianensium*" but PÉREZ & REYES (1989: 10) suggested it most likely came from the Valanginian at Puerta Curaco in Neuquén, Argentina, from where it was recorded by H.A. LEANZA & GARATE (1987). Here the specimen figured by H.A. LEANZA & GARATE (1987, pl. 13, figs. 1, 2), MOZ-P0917, is selected as neotype, and the type locality becomes Puerta Curaco with the type horizon the Mulichinco Formation of late Early Valanginian *Lissonia riveroi* and early Late Valanginian *Olcostephanus atherstoni* zones. We interpret *Weaverella* n.g. to include the *steinmanni* group (C) of REYES et al. (1981).

Genus *Neuquenella* nov.

Etymology: From Neuquén (Argentina), the province from where the type species was collected in the Pilmatué Member of the Agrio Formation.

Type species: *Steinmanella (Macrotrigonia) pehuenmapuensis* H.A. LEANZA (1998: 57, pl. 1, figs. 1-7; LAZO 2003: 1076, figs. 6.1-6.11; LAZO & LUCI 2013: 70, fig. 6); by original designation herein.

Neuquenella pehuenmapuensis (H.A. LEANZA, 1998)
Fig. 4I, J

Diagnosis for genus: Moderately large, subtrigonal, with prominent terminal umbones, straight vertical anterior margin, flat narrow anterior face crossed by concave-up rib terminations, and short, straight posterodorsal margin; escutcheon not sunken, fastigiate on conjoined valves; curved flank costae strongly oblique, mostly intersecting anterior margin, sometimes forming enlarged double nodes on anterolateral shoulder. *Late Late Valanginian*.

Referred species: *N. kensleyi* (COOPER 1979: 58, fig. 8) (Fig. 4M).

Discussion: Pandemic to the Andean (Argentina) and Ethiopian (South Africa) provinces. *Neuquenella* n.g. differs from *Weaverella* n.g. most obviously in its subtrigonal shape and straight vertical anterior margin, with irregular and sometimes enlarged tubercles along the anterior margin. *Neuquenella kensleyi* (Fig. 4M) differs from *N. pehuenmapuensis* in its smaller size and more-curved flank costae, with fused and doubled tubercles on the anterolateral shoulders separated by a short gap. This latter character is seen also in some specimens of *N. pehuenmapuensis* (cf. WEAVER 1931, pl. 21, fig. 106) and also younger (*Barremian*) *Pseudoyaadia hennigi* (LANGE) (see below). It was introduced as a species of *Macrotrigonia* but differs from the latter in its smaller size, vertical anterior margin and trigonal shape.

Genus *Steinmanella* CRICKMAY, 1930
= *Steinmannella* KOBAYASHI & AMANO, 1955, *nomen vanum*.
= *Steinmannaea* CRICKMAY, 1962, unnecessary replacement name.

Type species: *Trigonia holubi* KITCHIN 1908: 103, pl. 4, fig. 2; CAMACHO & OLIVERO 1985: 48, pl. 1, figs. 1, 2; COOPER 1991: 16, figs. 6-8; by original designation.

Steinmanella holubi (KITCHIN, 1908)
Fig. 4G

Diagnosis for genus: Large to very large, subquadratic to subrectangular, longer than high, with straight vertical to slightly procline anterior margin, small inconspicuous near-terminal umbones, perpendicular to obtuse umbonal angle and narrow unornamented anterior face with rounded shoulders; ventral and posterodorsal margins subparallel; ligament nymph large (1/L = 0.25); maximum inflation slightly anterior of anterolateral shoulders; escutcheon long, very narrow, with commarginal rows of ellipsoidal nodes, largest adjacent to commissure; in early to middle growth broad bipartite area unornamented but for conspicuous nodate inner, median and marginal carinae, nodes becoming elongated in middle growth and replaced by irregular

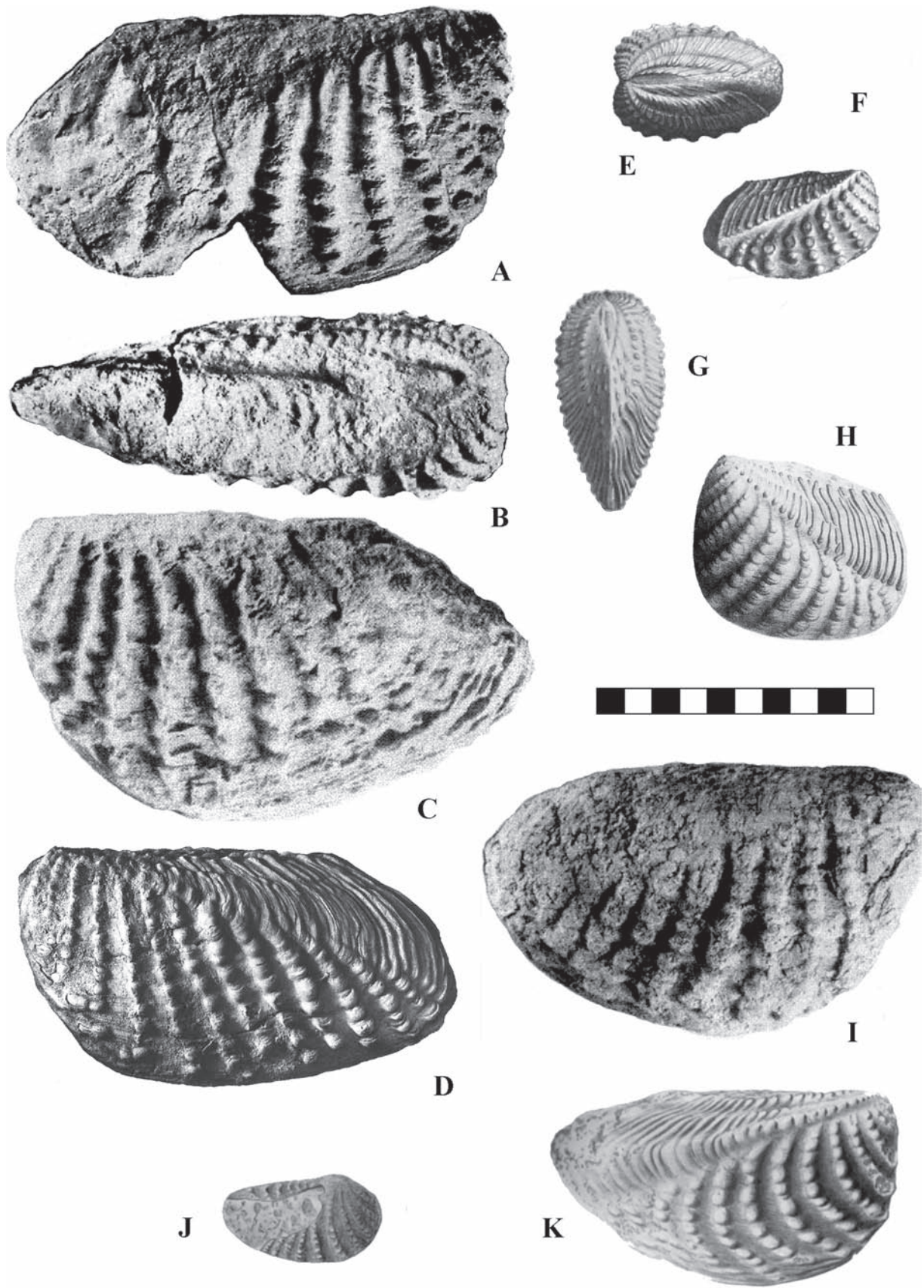


Fig. 5.

growth rugae in maturity; narrow antecarinal space in early to middle growth, becoming obsolete later with encroachment of tubercles from flank and rugae from area; flank costae moderately curved, mostly terminating along ventral margin, with crowded nodes increasing in size posteriorly but decreasing in size and becoming ellipsoidal ventrally; tuberculation somewhat irregular anteroventrally, sometimes with intercalated rows and enlarged nodes separated by gaps. *Early Late Valanginian*.

Referred species: *S. caicayensis* LAZO & LUCI (2013: 65, fig. 4) (Fig. 4K, L), *S. cf. caicayensis* LUCI & LAZO (= *Trigonia transitoria* STEINMANN 1882 (non 1881), after STEINMANN (1882) (Fig. 5G, H), *S. mamillata* (KITCHIN 1903: 100, pl. 9, figs. 8, 9, pl. 10, figs. 1-3) (Fig. 4H).

Discussion: *Steinmanella* is pandemic to the Andean and Ethiopian provinces (Argentina, South Africa, India). According to RUDRA et al. (2007) the type horizon of *S. mamillata* is Late Valanginian in age, not Tithonian-Berriasian as previously believed (COOPER 1979, 1991). Palaeobiogeographical considerations indicate that the progenitor of *S. mamillata* lies in some Ethiopian steinmanelline, with its subquadratic shape, straight vertical anterior margin (not preserved in the lectotype) and curved flank costae indicating assignment to *Steinmanella*, contrary to the view of CAMACHO & OLIVERO (1985).

Steinmanella differs from *Weaverella* n.g. in its larger size, subquadratic to subrectangular shape with straight subvertical anterior margin, weakly curved ventral margin subparallel to posterodorsal margin, lesser inflation, relatively smaller ligament nymph, prominent inner, median and marginal carinae in early to middle growth with well-spaced nodes, and less-curved flank costae which become irregularly nodate anteriorly in later growth, with gaps and enlarged nodes.

Genus *Transitrigonia* DIETRICH, 1933

Type species: *Trigonia transitoria* STEINMANN 1881: 260, pl. 13, fig. 3; by monotypy.

Transitrigonia transitoria (STEINMANN, 1881)

Fig. 5E, F

Diagnosis of genus: Very large, massive, strongly inequilateral, elongate-ovate to subrectangular, with subparallel

posterodorsal and ventral margins and low insignificant umbones; anterior margin subvertical to opisthocline with acute umbonal angle, curving imperceptibly into long gently-convex ventral margin; escutcheon with commarginal or transverse rows of nodes; escutcheon carina with prominent nodes becoming increasing elongate in middle growth; area with commarginal costellae in earliest growth which evanesce later; nodate median carina becomes obsolete in later growth when irregular commarginal growth rugae cross area; marginal carina nodate, nodes becoming elongate in middle growth and obsolete in later growth when growth rugae from the area cross onto the posterodorsal flank; antecarinal sulcus in early to middle growth becoming obsolete later; flank costae weakly curved, almost straight, posteriorly opisthocline, mostly terminating along the ventral margin, effaced from anterior face; nodes to flank costae increase in size posteriorly. *Late Valanginian – Early Barremian*.

Referred species: *T. herzogi* (GOLDFUSS 1837: 193, pl. 137, fig. 5; STEINMANN 1882: 219, pls. 7-9; KITCHIN 1908: 101, pl. 5, fig. 1; CAMACHO & OLIVERO 1985: 53, pl. 2, fig. 2, pl. 3, fig. 3; COOPER 1991: 19, figs. 9-12) (Fig. 5D), *T. katterfeldensis* (CAMACHO & OLIVERO 1985: 53, pl. 2, figs. 3-4) (Fig. 5A, B), *T. maxima* (CAMACHO & OLIVERO 1985: 58, pl. 1, fig. 5, pl. 3, fig. 1) (Fig. 5C), *T. posadensis* (CAMACHO & OLIVERO 1985: 55, pl. 4, figs. 1, 3) (Fig. 5I), *T. vacaensis* (WEAVER 1931: 251, pl. 24, figs. 126-130; H.A. LEANZA 1993: 45, pl. 15, figs. 6-7, pl. 16, fig. 13) (Fig. 5K), *T. sp.* (= *herzogi* REYES (non GOLDFUSS) 1970: 15, pl. 3, figs. 2-3, pl. 4, figs. 1-3).

Discussion: *Transitrigonia* is pandemic to the Andean (Chile, Argentina) and Ethiopian (South Africa) provinces, with most species Middle to Late Hauterivian. It includes the A₂ group of REYES et al. (1981). The genus holds a special place in steinmanellid classification since the type species, together with *T. herzogi* GOLDFUSS, formed the basis for recognition of the group Pseudo-Quadratae, and corresponds to the A₁ group of REYES et al. (1981).

As interpreted here *Transitrigonia* differs from *Weaverella* n.g. most obviously in its very large size, posterior elongation with very long posterodorsal margin, subrectangular shape, straight anterior margin, subparallel posterodorsal and ventral margins, straighter more-distant flank costae which do not curve strongly forwards but terminate mostly along the ventral margin, and prominent rounded nodes to the flank costae that increase in size posteriorly.

Transitrigonia transitoria was based (STEINMANN 1881: 260, pl. 13, fig. 3) on a specimen said to have come from the Lower? Cretaceous of Caracoles, Bolivia. However, Caracoles is 55 km northeast of Antofagasta (c. S 23°02' –

Fig. 5. A, B – *Transitrigonia katterfeldensis* (CAMACHO & OLIVERO), the holotype after CAMACHO & OLIVERO (1985). **C** – *Transitrigonia maxima* (CAMACHO & OLIVERO), the holotype after CAMACHO & OLIVERO (1985). **D** – *Transitrigonia herzogi* (GOLDFUSS), the provisional neotype after COOPER (1991). **E, F** – *Transitrigonia transitoria* (STEINMANN), the holotype by monotypy, after STEINMANN (1881). **G, H** – *Steinmanella cf. caicayensis* LUCI & LAZO (= *Trigonia transitoria* STEINMANN 1882 (non 1881), after STEINMANN (1882)). **I** – *Transitrigonia posadensis* (CAMACHO & OLIVERO), the holotype after CAMACHO & OLIVERO (1985). **J** – “*Trigonia*” *amarali* PHILIPPI, the holotype by monotypy, after PHILIPPI (1899). **K** – *Transitrigonia vacaensis* (WEAVER), the lectotype designated herein, after WEAVER (1931).

W 69°) and thus actually in northern Chile. It was found in a similar grey marly limestone to *Heteraster oblongus* (DE LUC) and *Janira* sp. [= *Neithea* cf. *atava* (ROEMER)], the latter a typically Neocomian (Berriasian – Barremian) species (DHONDT 1973). STOYANOW'S (1949: 69) subsequent selection of the original of STEINMANN (1882, pl. 8, fig. 3) (Fig. 5G, H) as lectotype is invalid, since STEINMANN'S (1881) specimen was the holotype by monotypy.

Although *T. transitoria* is a widely-cited Andean species, at present only the holotype can be assigned here with confidence. According to LAZO & LUCI (2013: 74) they received photographs of the holotype of *T. transitoria* from the Philipps-Universität Marburg (Germany), but our similar request went unanswered, both by the university and Dr LAZO. As illustrated by STEINMANN, the holotype of *T. transitoria* is medium-sized (L = c. 60 mm; measured from the plate and assumed to be figured approximately in natural size like the ammonite on the same plate), small for a steinmanellid and hence probably immature. It is posteriorly very elongate (H/L = 0.63), subrectangular, with maximum inflation close to midlength (W/H = 0.34), and with small, low, anteriorly-positioned umbones, moderately-incurved beaks and a broad anterior face with rounded anterolateral shoulders. The almost straight, subvertical anterior margin curves evenly into the long gently-convex ventral margin which is subparallel to the long, straight posterodorsal margin; the respiratory margin is obliquely subtruncate. There is a large ligament nymph (l/L = 0.39), much longer than wide (w/l = 0.10). The escutcheon is relatively large, shallowly sunken, with indistinct (?due to erosion), elongate, commarginal nodes. The nodes to the escutcheon carina become increasingly elongate posteriorly, eventually passing into the growth rugae of the area. In early to middle growth the bipartite area has a prominent longitudinal furrow flanked by a nodate median carina, the nodes becoming absorbed by commarginal growth rugae in later growth. The marginal carina is nodate, the nodes not increasing markedly in size posteriorly. There is a shallow antecarinal sulcus which persists to the posterior margin and is not crossed by growth rugae from the area. There are feeble, very short, opisthocline dorsal stems to the flank costae which are distant, slightly curved, and coarsely tuberculate, with only four tubercles per rib at midlength. The ribs are narrower than the interspaces, with tubercles increasing in size posteriorly, and most (66%) terminating along the ventral margin. Factors which suggest the holotype is immature include its relatively small size, persistent antecarinal sulcus and areal rugae failing to cross onto the posterodorsal flank.

In our view, *T. transitoria* has been badly misinterpreted by previous workers. Material subsequently referred to this species by its author (STEINMANN 1882: 221, pl. 7, figs. 3, 4, pl. 8, figs. 1-3) (Fig. 5G, H), and on which interpretation of the species has been based, came from the Bío Bío region, some 1400 km to the south of Caracoles, at the same latitude as the Argentinean Neuquén Basin. It comprised 5 fairly well-preserved specimens in the collection of the former Mining Office in Munich (but these could not be found by Dr S. SCHNEIDER, in litt.), from three different localities as follows: 2 specimens from Cordillera (Nevados) de Chillán (S 36°18'), together with *Ptychomya*, 1 specimen from Baños de Chillán, and 2 specimens from near the Antuco volcano

(S 37°16'). All were from unknown stratigraphical levels and different localities to the holotype and hence cannot be regarded as topotypes. Their true identity awaits re-analysis. We place the material assigned to *S. transitoria* by LUCI & LAZO (2012) in *Weaverella* n.g.

As recognized by STEINMANN (1881), and confirmed by morphometrical analysis (REYES et al. 1981), *T. transitoria* is closely allied to South African *T. herzogi*, a species placed in the subgenus *Macrotrigonia* by CAMACHO & OLIVERO (1985). The latter taxon was introduced for the Hauterivian *S. (M.) katterfeldensis* (Fig. 5A, B), which seems to differ from *T. herzogi* mainly in its younger age, curved flank costae and in having subtransverse costellae to the escutcheon. The ornament of the escutcheon is unknown in the other two species assigned to the subgenus by CAMACHO & OLIVERO (1985), and both *T. herzogi* and *T. vacaensis* differ in having commarginal rows of nodes. Moreover, immature *T. maxima* (CAMACHO & OLIVERO 1985, pl. 1, fig. 5) has a strongly convex ventral margin and looks much like a very large *Weaverella* n.g. For the present we treat *Macrotrigonia* as a synonym of *Transitrigonia* but better knowledge of the Argentine material, which is from the Middle Hauterivian to Early Barremian, is required.

Transitrigonia herzogi, the earliest species in the genus (early Late Valanginian), shares with *Steinmanella* a heavy robust shell, unornamented anterior face, subparallel ventral and posterodorsal margins, and flank costae that become irregularly nodate anteroventrally, with variable gaps and enlarged nodes. We believe they are sister taxa.

Genus *Pseudoyaadia* nov.

Etymology: The generic name refers to its superficial (convergent) resemblance to *Yaadia*.

Type species: *Trigonia hennigi* LANGE (1914: 238, pl. 19, fig. 3; RENNIE 1936: 347, pl. 43, figs. 1-3, pl. 44, fig. 1), by original designation herein.

Pseudoyaadia hennigi (LANGE, 1914)

Fig. 6J

Diagnosis for genus: Large (Lmax = 130 mm), posteriorly elongate (H/L = 0.63), ovate, with low, inconspicuous, near-terminal umbones and small incurved opisthogyrous beaks; anterior margin gently convex, inclined, with acute umbonal angle and flat, narrow, unornamented anterior face; long (l = 28 mm) narrow lunule (w/l = 0.25); anteroventral corner rounded, ventral margin convex, broad oblique respiratory margin gently convex, and long posterodorsal margin straight; ligament nymph relatively long (l = 32 mm), narrow (w/l = 0.18); escutcheon relatively broad, in early growth with transverse nodate costae, the nodes becoming smaller and oblique in middle growth and hence commarginal; in earliest growth area with commarginal costellae with prominent nodate escutcheon, median and marginal carinae, nodes of median and marginal carinae obsolete in middle to later growth when area is ornamented by growth striae only; curved flank

costae oblique, narrower than interspaces, with large rounded nodes, about half terminating on anterolateral shoulder in a disconnected double row of enlarged tubercles. *Barremian*.

Discussion: *Pseudoyaadia* n.g. is endemic to the Ethiopian (Zululand, Tanzania) Province. Superficially it greatly resembles *Yaadia* but their disjunct distribution and vast geographical separation suggests the similarity is due to convergence. However, the possibility that it may be a case of bipolar distribution (cf. DAMBORENEA et al. 2013) should be investigated. It differs from *Yaadia* most obviously in lacking bar-like ribs to the inner area in early growth. In addition it differs in being larger, with an acute umbonal angle, rounded anterolateral corner, sparser more-distant flank costae and the early loss of median and marginal carinae. It differs from all other Steinmanellinae in lacking irregular growth rugae to the area. *Pseudoyaadia* n.g. appears above a stratigraphical discontinuity and hence its immediate antecedent is unknown. However, its acute umbonal angle, sparse flank costae terminating mainly along the ventral margin, and transverse costae to the escutcheon are features of some *Transitrigonia*, e.g. *T. katterfeldensis* (CAMACHO & OLIVERO (1985)), and a double row of tubercles along the anterolateral shoulder is a feature of *Neuquenella kensleyi* (COOPER).

Subfamily Yaadiinae nov.

Diagnosis: Moderately large, mostly subovate, with small low anteriorly-positioned umbones and opisthogyrous beaks; straight vertical to rounded anterior margin, convex ventral margin, obliquely-subtruncate respiratory margin and long shallowly-concave to almost-straight posterodorsal margin; escutcheon moderately wide, shallowly-sunken with transverse costellae which evanesces medially in derived members; nodate inner and marginal carinae, evanescing in middle to later growth in derived members; commarginal ribs of inner area in early growth persist in middle to later growth as bar-like transverse nodes on inner carina; area with growth striae only in middle to later growth; flanks with curved rows of uniform nodes, primitively enlarged on anterolateral shoulder. ?*Middle Valanginian, Hauterivian – Maastrichtian*.

Discussion: Yaadiines are restricted to the Boreal Realm. They first appeared in the Middle Valanginian of the Cordilleran Province (northern California, Oregon, British Columbia, Queen Charlotte Island), from where they spread into the Oriental Province (Japan) in the Cenomanian. The subfamily persisted into the Maastrichtian in both provinces, and its origin has been inferred to lie in Steinmanellinae (COOPER 1991). Since transverse costellae to the escutcheon are a character shared both with *Splenditrigonia* and *Stoyanowella* n.g., palaeobiogeographical considerations suggest an early split from Steinmanellinae and that the origin of Yaadiinae nov. may in fact lie close to Kimmeridgian *Stoyanowella* n.g.

Typically yaadiines are found in medium- to coarse-grained, immature, pebbly sandstones of nearshore high-energy environments (inner sublittoral zone) suggestive of

water depths of 7–40 m, "... and are absent from the finer grained more basinward deposits" (SAUL 1978: 17). Thus their ecological requirements are different from most steinmanellines.

Genus *Yaadia* CRICKMAY, 1930

Type species: *Trigonia lewisagassizi* CRICKMAY 1930: 50, pl. 13, figs. 1, 2; SAUL 1991: 27, text-figs. 8, 10; by original designation.

Yaadia lewisagassizi (CRICKMAY, 1932)

Fig. 6A, B

Diagnosis of genus: Moderately large to large, thick-shelled, subquadratic, longer than high with subterminal umbones and opisthogyrous beaks; straight vertical anterior margin, long gently-convex ventral margin, obliquely subtruncate respiratory margin and long essentially straight posterodorsal margin; anterior face flat, with extensions of flank costae; escutcheon relatively broad, subtabulate, extending most of posterodorsal length, with transverse or commarginal rows of beads, or smooth; inner carina with strong, bar-like transverse nodes which in early growth extend across inner area to reach longitudinal furrow; bipartite area with persistent, nodate, median and marginal carinae, ornamented only in early growth with transverse bars from escutcheon on inner part, and fine commarginal) costellae on outer part; narrow unornamented antecarinal space; flanks with nodate commarginal costellae in early growth, later with 1–2 vertical rows of enlarged tubercles on anterolateral shoulders more-or-less separated from weakly-curved, oblique flank costae with large rounded to ellipsoidal nodes. ?*Middle Valanginian, Hauterivian – Cenomanian*.

Referred species: *Y. jonesi* SAUL (1978: 29, pl. 1, figs., 1–8, pl. 2, figs. 1, 2, pl. 11, fig. 1, text-fig. 11) (Fig. 6C), *Y. leana* (GABB 1876: 312; = *Trigonia gibboniana* GABB (non LEA) 1864: 190, pl. 25, fig. 178, pl. 31, fig. 262; SAUL 1978: 33, pl. 4, figs. 1–8, pl. 5, figs. 1–4, pl. 11, fig. 2, text-fig. 13a, b; = *Trigonia colusaensis* ANDERSON 1958: 110, pl. 1, fig. 6; = *Trigonia wheelerensis* ANDERSON 1958: 116) (Fig. 6F, G), *Y. whiteavesi* (PACKARD 1921: 21, pl. 6, fig. 2 only; SAUL 1978: 31, pl. 2, figs. 3–5, pl. 3, figs. 1–6, text-fig. 12; = *Trigonia per-rinsmithi* ANDERSON 1958: 110, pl. 2, fig. 7) (Fig. 6D).

Discussion: *Yaadia* is typical of the Cordilleran Province (British Columbia, Oregon, northern California). Due to poor knowledge of the type species, recognized only by the tectonically-distorted holotype, some might regard *Yaadia* as a *nomen dubium*. However, it is clearly congeneric with slightly younger *Y. jonesi* SAUL (Fig. 6C) which, in our opinion, validates the generic characteristics of *Yaadia*. Although a poorly-known species *Y. lewisagassizi* differs from its immediate descendent and closest ally, *Y. jonesi*, in having two rows of enlarged shoulder tubercles rather than just one. Future work may show these differences represent no more than intraspecific variation and, with better material, the two species may be shown to be conspecific.

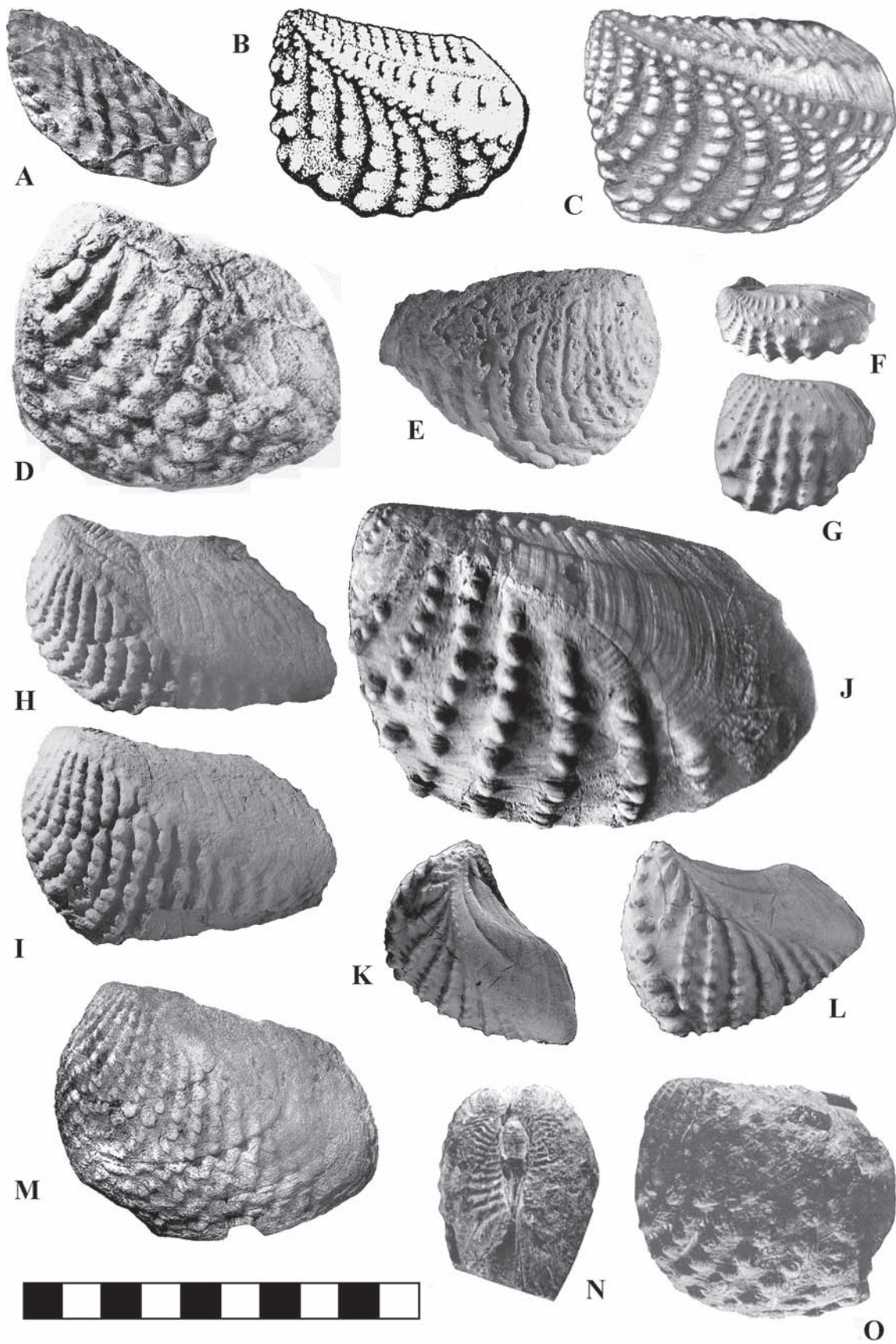


Fig. 6.

A feature not emphasized by SAUL (1978), but clearly evident in the Middle to Late Hauterivian *Y. jonesi* (SAUL 1978, pl. 1, fig. 8) (Fig. 6C) and in the Early Albian *Y. whiteavesi* (POULTON 1977, pl. 1, figs. 14, 15) (Fig. 6D) are subtransverse rows of beaded costellae to the escutcheon. This primitive character, shared with *Stoyanowella* n.g. and *Splenditrigonia*, is less consistent in *Y. leana* (GABB) but is still displayed by some individuals (SAUL 1978, pl. 4, fig. 4).

Yaadia has a superficial resemblance to the myophorelline *Scaphotrigonia* (Fig. 6K, L), but the latter is smaller, with an unornamented escutcheon and straighter flank costae, and lacks a median nodate carina and nodate escutcheon and marginal carina which are present only in early growth. We regard the similarity as due to convergence.

The species *lewisagassizi* → *jonesi* → *whiteavesi* → *leana* form a Middle Valanginian to Early Turonian evolutionary series. *Yaadia* differs from its possible progenitor *Stoyanowella* n.g. in its straight subvertical anterior margin, near-terminal umbones and doubled rows of enlarged tubercles to the anterolateral shoulders. It differs from *Steinmanella* in its smaller size, narrower more-rounded respiratory margin, curved marginal carina, sparser, more distant flank costae with 1-2 well-developed vertical rows of enlarged tubercles on the anterolateral shoulders, lack of growth rugae to the area in later growth and presence of bar-like transverse nodes to the inner area and escutcheon carina.

Genus *Popenoella* nov.

= *Packardella* KOBAYASHI & AMANO, 1955, a *nomen nudum*.

Etymology: For W.P. POPENOE, in recognition of his work on the Cretaceous stratigraphy and palaeontology of the Pacific Coast of North America.

Type species: *Trigonia hemphilli* ANDERSON 1958: 115, pl. 52, fig. 9; SAUL 1978: 50, pl. 10, figs. 2-9, pl. 11, figs. 3, 6, text-figs. 8, 19; by original designation herein.

Popenoella hemphilli (ANDERSON, 1958)

Fig. 6N, O

Diagnosis of genus: Like *Yaadia* but with rounded anterolateral margin, umbones positioned further back, anterior

face not flattened, rounded anterolateral shoulders without enlarged tubercles; narrow shallowly-sunken escutcheon smooth (primitive), or with strong subtransverse costellae continuous from area (derived); very large ligament nymph; juvenile ribbing of area may form complicated chevrons; nodate marginal carinae evanescent in later growth. *Late Turonian* – *Early Maastrichtian*.

Referred species: *P. branti* SAUL (1978: 43, pl. 7, figs. 3-10, pl. 8, fig. 1, pl. 11, fig. 5, text-fig. 16), *P. californiana* (PACKARD 1921: 17, pl. 2, fig. 2; SAUL 1978: 39, pl. 5, figs. 5-8, pl. 6, figs. 1, 2, pl. 11, fig. 4, text-fig. 14), *P. pinea* SAUL (1978: 42, pl. 6, figs. 3-6, pl. 7, figs. 1, 2, text-fig. 15), *P. robusta* (SAUL 1978: 47, pl. 9, figs. 2-4, 6, text-fig. 18), *P. tryoniana* (GABB 1864: 188, pl. 25, fig. 176; WHITEAVES 1879: 161, pl. 18, fig. 7; PACKARD 1921: 19, pl. 4, fig. 4; SAUL 1978: 45, pl. 8, figs. 2-7, pl. 9, fig. 1, text-fig. 17).

Discussion: *Popenoella* n.g. is endemic to the Cordilleran Province (northern California, Oregon, British Columbia), quite obviously with an origin in *Yaadia*. SAUL (1978: 27) declined to name this group on the grounds that "...it tends to obscure their direct relationship to *Yaadia*". The writers have the opposite view, that this genus is necessary to taxonomically reflect the significant evolutionary change within this lineage. Quite obviously the primitive species more closely approach ancestral *Yaadia*, but the two genera become increasingly divergent with time so that Maastrichtian *P. hemphilli* is very different from *Y. lewisagassizi* and *Y. jonesi*. Its sparser costation and coarse flank tubercles immediately distinguish it from *Louella* n.g.

KOBAYASHI & AMANO (1955: 193) considered the species *californiana*, *tryoniana*, *fitchi*, *leana* and *whiteavesi* an endemic group closely allied to, but distinct from, Japanese *Yeharella*. They distinguished the North American group as a "*Packardella* section" in which "" the effacement of the sculpture was more advanced" (p. 198). While we recognize this grouping also, unfortunately they failed to designate a type species and their name is a *nomen nudum*.

The holotype of *P. tryoniana* (GABB) has a very different aspect to the other species of *Popenoella* n.g., with subdued flank ornament and two conspicuous radiating grooves which correspond to the antecarinal sulcus and the longitudinal furrow to the area. This is due to exfoliation of the outermost shell layer (cf. SAUL 1978). Likewise the lost holotype of *P. californiana* (PACKARD) also seems to have had the outermost shell layer exfoliated, and problems associated with its identification were dealt with by SAUL (1978).

Fig. 6. A, B – *Yaadia lewisagassizi* CRICKMAY; A, the holotype after CRICKMAY (1932); B, a reconstruction after SAUL (1978). **C.** *Yaadia jonesi* SAUL, a restoration. **D** – *Yaadia whiteavesi* (PACKARD), the lectotype designated herein, after POULTON (1977). **E, H, I, M** – *Louella fitchi* (PACKARD). E, cast of the holotype, UO-26859; H-I, cast of the paratype, UO-26910; M, the holotype of *Trigonia branneri* ANDERSON, after ANDERSON (1958). **F, G** – *Yaadia leana* (GABB), USNMNH-241677, a juvenile showing the bar-like ribs to the outer area and inner escutcheon, an apomorphic character for Yaadiinae. **J** – *Pseudoyaadia hennigi* (LANGE), the unnumbered SAM specimen figured by RENNIE (1936) from the Barremian of Zululand. **K, L** – *Scaphotrigonia navis* (LAMARCK), an unnumbered BMNH specimen. **N-O** – *Popenoella hemphilli* (ANDERSON), the holotype, after ANDERSON (1958).

Genus *Louella* nov.

Etymology: For Dr LOUELLA R. SAUL (Los Angeles County Museum), eminent American malacologist and monographer of the genus *Yaardia*.

Type species: *Trigonia fitchi* PACKARD 1921: 20, pl. 6, fig. 3, pl. 7, fig. 2; = *T. branneri* ANDERSON 1958: 112, pl. 17, fig. 5 (Fig. 6M); by original designation herein.

Louella fitchi (PACKARD, 1921)

Fig. 6E, H, I, M

Diagnosis for genus: Moderately large, elongate-subovate, with insignificant subterminal umbones and convex anterior margin; anterior face fastigate; respiratory margin obliquely subtruncate; long posterodorsal margin straight shallowly sunken; escutcheon large, shallowly sunken, in early growth with bar-like transverse costae (primitive) or fine oblique costellae continuous from area (derived), later unornamented and not discriminated from area, fastigate on conjoined valves; inner carina non-tuberculate, marked only by change in slope; area broad, convex, with fine oblique costellae in early growth; longitudinal furrow to area present only in early growth; curved flank costae numerous, broader than interspaces, with small uniform nodes, in later growth cutting obliquely across the growth striae anteriorly and forming zigzags ventrally. *Early – Middle Turonian*.

Description: The holotype is medium-sized (L = 68 mm), elongate-ovate, strongly inequilateral, longer than high (H/L = 0.81), inflated (W/H = 0.46), with low subterminal umbones. The subvertical anterior margin passes rapidly into the moderately-convex ventral margin, the respiratory margin is not preserved, but growth striae indicate it was obliquely subtruncate, and the long posterodorsal margin is very-shallowly sunken. The escutcheon is defined only in earliest growth, with transverse bars, later not discriminated from the area. The broad flat area has nodate carinae only in earliest growth, later with commarginal striae only. The flanks are ornamented with 15 conspicuous, curved oblique costae, broader than the interspaces, bearing regularly-disposed, crowded, small nodes. The holotype of *T. branneri* ANDERSON shows the flank costae becoming zigzag anteroventrally in later growth (Fig. 6M).

Referred species: *L? jimboi* (KOBAYASHI & AMANO 1955: 204, pl. 13, fig. 4).

Discussion: This genus is known with certainty only from the Cordilleran Province (Oregon, northern California), but may be present also in the Oriental Province (Japan). As noted by SAUL (1978: 13), *Trigonia fitchi* "... is obviously not a *Yaardia*". She tentatively assigned it to *Litschkovitrigonia*, but the latter is a member of *Quadratotrigoniinae* endemic to the Central Asian Province with V-shaped flank costae in early growth. The transverse bars to the escutcheon of *L. fitchi* point to an origin in *Yaardia*.

Louella n.g. differs from *Yaardia* in its convex anterior margin, fastigate anterior face and posterodorsal region on

conjoined valves, round anterolateral shoulders without enlarged tubercles, escutcheon non-discriminated in middle to later growth, early loss of nodate carinae to the area, and numerous, closely-spaced flank costae with crowded uniform nodes.

SAUL (1978: 53, pl. 12, figs. 2-7, text-fig. 20) figured Turonian material from the Hornbrook Formation, Siskiyou County, Klamath River, California, as *L? fitchi*. However, it differs from the holotype of *L. fitchi* in having fine diagonal costellae to the escutcheon and area in early to middle growth. Whether this is due to better preservation, or a different species is involved, remains to be determined.

Densicostate *Steinmanella* (*Yeharella*) *jimboi* KOBAYASHI & AMANO (1955: 204, pl. 13, fig. 4) is based on an internal mould which has been assigned tentatively to *Litschkovitrigonia* (SAUL 1978; TASHIRO & MOROZUMI 1982), but the latter genus is an Asiatic endemic. Poor illustration and inadequate description hinder proper identification of *Y. jimboi* but dense geniculate ribbing suggests it may belong here. Just as likely, however, the similarity could be due to convergence.

Genus *Yeharella* KOBAYASHI & AMANO, 1955

Type species: *Trigonia japonica* YEHARA 1923a: 10, pl. 6, figs. 6, 7; 1923b: 83, pl. 12, figs. 3, 4; KOBAYASHI & AMANO 1955: 201, pl. 14, figs. 1-3, pl. 15, fig. 4; HAYAMI 1975: 112, pl. 5, fig. 12; = *sanukiensis* NAKANO 1958: 86, pl. 13, fig. 1; by original designation.

Yeharella japonica (YEHARA, 1923a)

Fig. 7

Diagnosis of genus: Moderately large to large, subquadratic to subovate, longer than high, with low insignificant anteriorly-positioned umbones; anterior and ventral margins convex, oblique respiratory margin gently convex, long posterodorsal margin shallowly concave to straight; escutcheon narrow, shallowly sunken, with oblique costellae meeting at commissure in posteriorly-directed chevrons; inner, median and marginal carinae nodate in early to middle growth, evanescent later with rounding of marginal carina; broad bipartite area with commarginal costellae in earliest growth, later with growth striae only; narrow antecarinal space, evanescent in later growth; strongly-curved nodate flank costae, narrower than interspaces, most terminating along anterior commissure, nodes tending to elongate and coalesce in later growth to become segmented subcommarginal cords. *Cenomanian – Maastrichtian*.

Referred species: *Y. ainuana* (YABE & NAGAO 1928: 84, pl. 16, fig. 20; KOBAYASHI & AMANO 1955: 204), *Y. deckeina* (KUBOTA 1955: 14, pl. 1, figs. 1, 2; NAKANO 1958: 87, pl. 13, fig. 2, pl. 14, fig. 1), *Y. kimurai* (TOKUNUGA & SHIMIZU 1926: 189, pl. 27, figs. 3, 4; KOBAYASHI & AMANO 1955: 205, pl. 13, figs. 1, 2), *Y. lymani* (KOBAYASHI & AMANO 1955: 203, pl. 13, fig. 3), *Y. obsoleta* (KOBAYASHI & AMANO 1955: 202, pl. 14, figs. 4, 5), *Y. sinoharai* (KOBAYASHI & AMANO 1955: 207, pl. 15, figs. 1-3; HAYAMI 1975: 114, pl. 5, fig. 13).

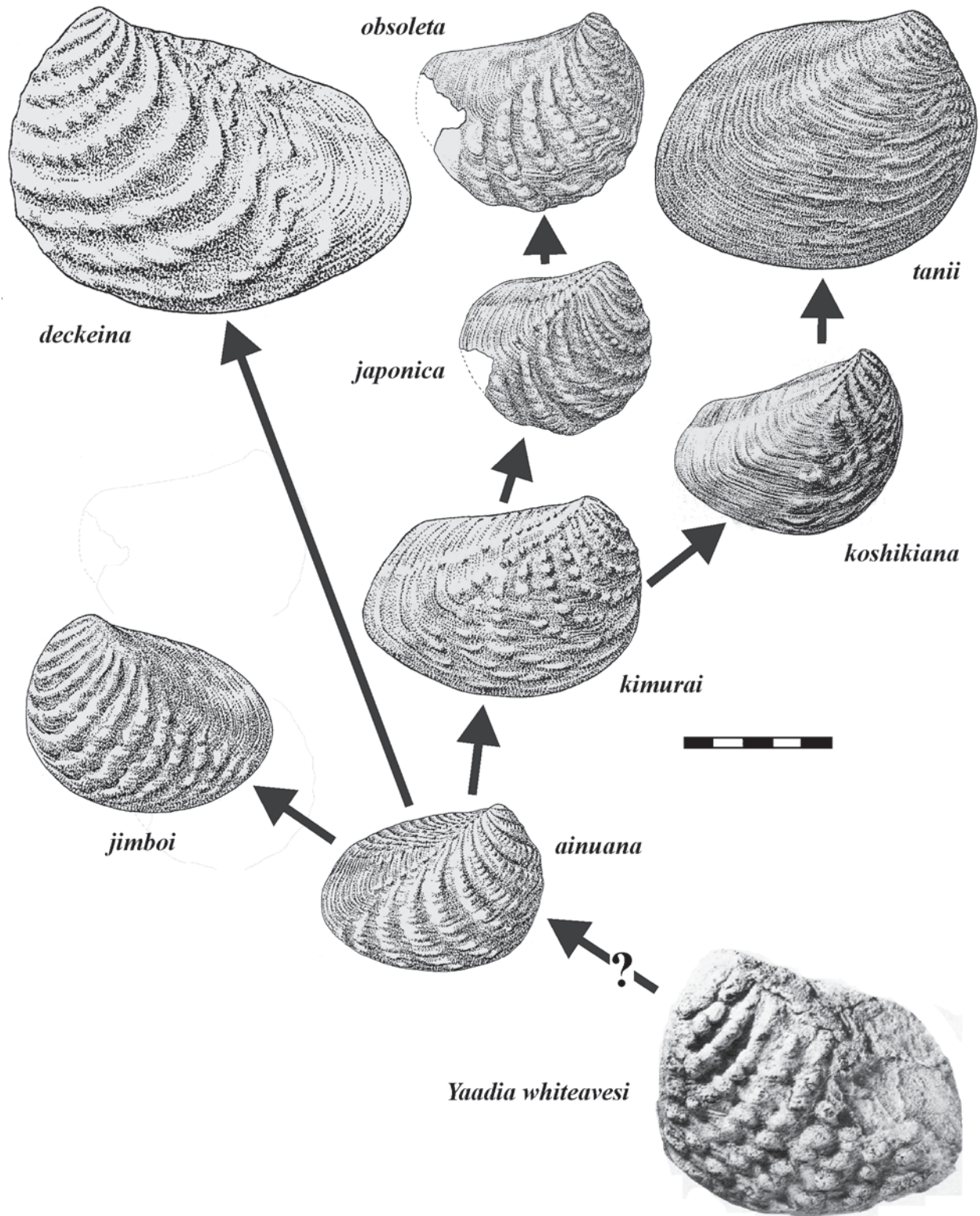


Fig. 7. Hypothesized relationships among species of *Yeharella* and *Tashiroella* n.g., adapted from TASHIRO & KANO (1989) and TASHIRO (1992). Note the significant phenotypic discontinuity separating Cenomanian *Yeharella ainuana* (JIMBO) and Albian *Yaadia whiteavesi* (PACKARD).

Discussion: *Yeharella* is an Oriental endemic (Japan). KOBAYASHI & AMANO (1955) looked to *Steinmanella* for the origin of the genus, whereas SAUL (1978) favoured *Yaadia*. The writers reject the suggestion (SAUL 1978; TASHIRO 1992) that *Yeharella* is a synonym of *Yaadia* since it constitutes a divergent Oriental group that evolved in parallel with other steinmanellid lineages. According to TASHIRO & KANO (1989) *Yeharella* comprises 3 lineages (clades) which evolved in parallel for much of the later Cretaceous, one of which is here made the basis of a new genus. The taxonomic status of the other two lineages remains to be determined.

Yeharella is first known from the Cenomanian-Turonian (TASHIRO 1988) and hence, if its ancestry lies in *Yaadia*, must be sought in older species of *Yaadia*, in particular the Albian-Cenomanian *Y. whiteavesi* (PACKARD) (Fig. 6D). However, the earliest *Yeharella*, *Y. ainuana*, differs markedly from *Y. whiteavesi* in its smaller size, ovate shape, convex anterior without flattened anterior face, lack of bar-like transverse nodes to the inner area which persist as the inner carina in middle to later growth, lack of enlarged tubercles on the anterolateral shoulders and gap separating them from the remainder of the flank, and fine oblique costellae to the area and escutcheon. The differences point to a moderate phenotypic discontinuity and derivation of *Yeharella* from *Yaadia* is conjectural rather than compelling.

Barremian *Pseudoyaadia hennigi* (LANGE) is the only Gondwanic steinmanellid that can be entertained as a candidate for the ancestor of *Yeharella*. However, it differs from *Y. ainuana* in its large size, very robust shell, subrectangular shape, with straighter more-distant flank costae with larger well-discriminated nodes, prominent nodate inner carina which persists almost to maturity, enlarged anterolateral shoulder tubercles, and coarse transverse costellae to the escutcheon. The two are separated by a moderate phenotypic discontinuity and vastly disjunct distributions.

Steinmanella (Setotrigonia) kobayashii (KOBAYASHI & AMANO 1955) was introduced as a monotypic subgenus for a species from the Campanian of Japan. However, TASHIRO & MOROZUMI (1982: 6, 7) pointed out that the holotype of *S. sinoharai* (KOBAYASHI & AMANO) is based on the external mould of a left valve, not a right valve as interpreted by KOBAYASHI & AMANO (1955). Hence it is the anterior not posterior part of a valve. Consequently they judged *S. sinoharai* "... not to be so different from *Yaadia japonica* (YEHARA)", which is from the same stratigraphical level. Here *Setotrigonia sinoharai* is considered a *nomen dubium*, and *Setotrigonia* is regarded as a subjective junior synonym of *Yeharella*.

Genus *Tashiroella* nov.

Fig. 7

Etymology: For Professor MASAYUKI TASHIRO (Kochi University), pre-eminent expert on Japanese Mesozoic bivalves.

Type species: *Yaadia tanii* TASHIRO & MOROZUMI 1982: 5, pl. 3, fig. 1; TASHIRO 1992: 146, pl. 39, fig. 7; by original designation herein.

Tashiroella tanii (TASHIRO & MOROZUMI, 1982)

Fig. 7

Diagnosis of genus: Like *Yeharella* but with very narrow, short, unornamented escutcheon; nodate inner, median and marginal carinae restricted to early growth (primitive) or obsolete (derived); broad bipartite area unornamented; nodate flank costae covering entire flank in early growth, evanescent posteriorly in middle to later growth. *Campanian* – *Maastrichtian*.

Referred species: *T. koshikiana* (TASHIRO & KANO 1989: 7, pl. 1, figs. 1-3, pl. 2, figs. 1-4, pl. 3, fig. 1, text-fig. 2; TASHIRO 1992: 150, pl. 45, fig. 7, erroneously labelled *Y. koshikijimensis*).

Discussion: Endemic to the Oriental Province (Japan). The type species is markedly different from contemporaneous species of *Yeharella*, i.e. *Y. obsoleta* (KOBAYASHI & AMANO) and *Y. japonica* (YEHARA), and *Popenoella* n.g., i.e. *P. hemphilli* (ANDERSON), and obviously represents the end members of a different phyletic line. TASHIRO & KANO (1989) looked to Coniacian *Yeharella kimurai* (KOBAYASHI & AMANO) for the origin of the genus, implying that *Yeharella* and *Tashiroella* n.g. evolved in parallel for much of the later Cretaceous.

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References

- AGASSIZ, L. (1840): Études critiques sur les mollusques fossiles. – Mémoire sur les trigonies. – 58 pp.; Neuchâtel (Petitpierre).
- ALBRITTON, C.C. (1937): The age of the Malone fauna. – Publication of the Shuler Museum, Field & Laboratory, 5 (2): 48-50.
- ANDERSON, F.M. (1938): Lower Cretaceous deposits in California and Oregon. – Geological Society of America, Special Papers, 16: 1-339.
- ANDERSON, F.M. (1958): Upper Cretaceous of the Pacific Coast. – Geological Society of America, Memoirs, 71: 1-378.

- BENETT, E. (1831): A catalogue of the organic remains of the county of Wilts. – Warminster (Vardy).
- BURCKHARDT, C. (1900a): Profils géologiques transversaux de la Cordillere Argentino-chilienne. – *Anales del Museo de La Plata, Sección Geológica y Mineralógica*, **2**: 1-136.
- BURCKHARDT, C. (1900b): Coupe géologique de la Cordillere entre Las Lajas et Curacautin. – *Anales del Museo de La Plata, Sección Geológica y Mineralógica*, **3**: 1-102.
- BURCKHARDT, C. (1903): Beiträge zur Kenntniss der Jura- und Kreideformation der Cordillere. – *Palaeontographica*, **50**: 1-144.
- CAMACHO, H.H. & OLIVERO, E.B. (1985): El género *Steinmanella* CRICKMAY, 1930 (Bivalvia, Trigoniidae) en el Cretácico Inferior del sudoeste gondwánico. – *Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales*, **37**: 41-62.
- COOPER, M.R. (1979): Cretaceous Trigoniidae (Mollusca, Bivalvia) from the Brenton Formation, Knysna. – *Annals of the South African Museum*, **78** (6): 49-67.
- COOPER, M.R. (1991): Lower Cretaceous Trigonioida (Mollusca, Bivalvia) from the Algoa basin, with a revised classification of the order. – *Annals of the South African Museum*, **100** (1): 1-52.
- COOPER, M.R. (2011): *Austromyophorella*, a new genus of Lower Cretaceous trigonioid bivalve from South Africa. – *Durban Museum Novitates*, **34**: 35-38.
- COOPER, M.R. (2015): On the Pterotrighoniidae (Bivalvia, Trigoniida): their biogeography, evolution, classification and relationships. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **277**: 11-42.
- CORVALÁN, J. & PÉREZ, E. (1958): Fósiles guías chilenos. Titoniano-Neocomiano. – *Instituto de Investigaciones Geológicas de Chile, Manual*, **1**: 1-48.
- COX, L.R. (1952): Notes on the Trigoniidae, with outlines of a classification of the family. – *Proceedings of the Malacological Society of London*, **29** (2-3): 45-70.
- COX, L.R. (1969): Trigoniacea LAMARCK, 1859. – In: MOORE, R.C. (Ed.): *Treatise on Invertebrate Paleontology. Part N, Mollusca* 6(1): N471-N489; Boulder & Lawrence (Geological Society of America & University of Kansas Press).
- CRAGIN, F.W. (1893): A contribution to the invertebrate paleontology of the Texas Cretaceous. – *Annual Report of the Geological Survey of Texas*, **4**: 141-246.
- CRAGIN, F.W. (1897): Discovery of marine Jurassic rocks in southwestern Texas. – *The Journal of Geology*, **5**: 813-820.
- CRAGIN, F.W. (1905): Paleontology of the Malone Jurassic formation of Texas. – *United States Geological Survey, Bulletins*, **266** (C, 73): 1-172.
- CRICKMAY, C.H. (1930): Fossils from Harrison Lake area, British Columbia. – *National Museum of Canada, Bulletins*, **63**: 33-66.
- CRICKMAY, C.H. (1932): Contributions toward a monograph on the Trigoniidae. – *American Journal of Sciences*, **24**: 443-464.
- CRICKMAY, C.H. (1962): Gross stratigraphy of Harrison Lake area, British Columbia, Calgary and Alberta, Part 8: 1-12; Calgary (published by the author).
- DAMBORENEA, S.E., ECHEVARIA, J. & ROS-FRANCO, S. (2013): Southern hemisphere palaeobiogeography of Triassic-Jurassic marine bivalves. Dordrecht, Heidelberg, New York & London (Springer).
- DIETRICH, W.O. (1933): Zur Stratigraphie und Paläontologie der Tendaguruschichten. – *Palaeontographica, Supplement-Bände*, **7**: 1-86.
- DHOND, A.V. (1973): Systematic revision of the subfamily Neitheinae (Pectinidae, Bivalvia, Mollusca) of the European Cretaceous. – *Koninklijk Belgisch Instituut voor Natuurwetenschappen Verhandeling*, **176**: 1-101.
- DOUVILLÉ, H. (1910): Cephalopods argentins. – *Mémoires de la Société Géologique de la France*, **43**: 1-22.
- FELIX, J. (1891): Versteinerungen aus dem oberen Jura des Cerro de Titania bei Tlaxiaco im Staat Oaxaca. – *Palaeontographica*, **37**: 140-194.
- GABB, W.M. (1864): Description of the Cretaceous fossils. – *Geological Survey of California, Palaeontology*, **1**: 57-217.
- GABB, W.M. (1876): Notes on American Cretaceous fossils with descriptions of some new species. – *Proceedings of the Academy of Natural Sciences of Philadelphia*, (3), **28**: 276-324.
- GOLDFUSS, G.A. (1834-1840): *Petrefacta Germaniae, tam ea, Quae in Museo Universitatis Regiae Borussicae Fridericiae Wilhelmae Rhenanea, serventur, quam alia quaecunque in Museis Hoeninghusiano Muensteriano aliisque, extant, iconibus et descriptionibus illustrata. Abbildungen und Beschreibungen der Petrefacten Deutschlands und der angrenzenden Länder, unter Mitwirkung des Herrn Grafen Georg zu Münster, herausgegeben von August Goldfuss. 2, Divisio quarta. Molluscorum acephalicorum reliquiae. I. Bivalvia*: 65-286; Düsseldorf (Arnz & Co.).
- HAUPT, O. (1907): Beiträge zur Fauna des oberen Malm und der unteren Kreide in der argentinischen Cordillere. – *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände*, **23**: 187-236.
- HAYAMI, I. (1975): A systematic survey of the Mesozoic Bivalvia from Japan. – *The University Museum, University of Tokyo, Bulletins*, **10**: 1-249.
- IMLAY, R.W. (1980): Jurassic paleobiogeography of the conterminous United States in its continental setting. – *United States Geological Survey, Professional Papers*, **1062**: 1-133.
- KENT, D.V. & IRVING, E. (2010): Influence of inclination error in sedimentary rocks on the Triassic and Jurassic apparent polar wander path for North America and implications for Cordilleran tectonics. – *Journal of Geophysical Research*, **115**: 1-25.
- KITCHIN, F.L. (1903): The Lamellibranchiata. Genus *Trigonia*. The Jurassic fauna of Cutch. – *Memoirs of the Geological Survey of India, Palaeontologica Indica*, (9), **3** (2, 1): 1-122.
- KITCHIN, F.L. (1908): The invertebrate fauna and palaeontological relations of the Uitenhage Series. – *Annals of the South African Museum*, **7** (2): 21-250.
- KOBAYASHI, T. (1954): Studies on the Jurassic trigonians from Japan. Part 1. Preliminary notes. – *Japanese Journal of Geology and Geography*, **24**: 61-80.
- KOBAYASHI, T. & AMANO, M. (1955): On the Pseudoquadratae trigonians, *Steinmanella*, in the Indo-Pacific province. – *Japanese Journal of Geology and Geography*, **26** (3-4): 193-208.

- KUBOTA, K. (1955): Large *Trigonia* from Hakobuchi Sandstone. – *Syumino-Tigaku*, **5** (3): 14-15.
- LANGE, E. (1914): Die Brachiopoden, Lamellibranchiaten und Anneliden der *Trigonia schwarzi*-Schicht, nebst vergleichender Übersicht der Trigonien der gesamten Tendaguruschichten. – *Archiv für Biontologie*, **3** (4): 193-289.
- LAZO, D.G. (2003): The genus *Steinmanella* (Bivalvia, Trigonioida) in the lower member of the Agrio Formation (Lower Cretaceous), Neuquén Basin, Argentina. – *Journal of Paleontology*, **77** (6): 1069-1085.
- LAZO, D.G. (2009): Vida y obra de CHARLES EDWIN WEAVER (1880-1958) y su paso por la Cuenca Neuquina en los años '20. – *Revista de la Asociación Geológica Argentina*, **77** (6): 1069-1085.
- LAZO, D.G. & LUCI, L. (2013): Revision of Valanginian *Steinmanellinae* bivalves from the Neuquén Basin, west-central Argentina, and their biostratigraphic implications. – *Cretaceous Research*, **45**: 60-75.
- LAMBERT, L.R. (1944): Algunas trigonias del Neuquén. – *Revista del Museo de La Plata, n.s., Paleontología*, **2**: 357-397.
- LEANZA, A.F. (1941): Dos nuevas trigonias del Titoniense de Carrin-Curá, en el territorio del Neuquén. – *Notas del Museo de La Plata, Paleontología*, **6**: 225-233.
- LEANZA, A.F. & CASTELLARO, H. (1955): Algunos fósiles Cretácicos de Chile. – *Revista de la Asociación Geológica Argentina*, **10**: 179-213.
- LEANZA, H.A. (1993): Jurassic and Cretaceous trigoniid bivalves from west-central Argentina. – *Bulletins of American Paleontology*, **105**: 1-95.
- LEANZA, H.A. (1998): Una nueva especie de *Steinmanella* CRICKMAY (Bivalvia, Trigonioida) del Cretácico Inferior de la Cuenca Neuquina, Argentina. – *Revista Geológica de Chile*, **25**: 57-67.
- LEANZA, H.A. & GARATE, J.I. (1987): Faunas de trigonias (Bivalvia) del Jurásico y Cretácico Inferior de la Provincia del Neuquén, Argentina, conservadas en el Museo Juan Olsacher de Zapala. – In: VOLKHEIMER, W. (Ed.): *Bioestratigrafía de los sistemas regionales del Jurásico y Cretácico de América del Sur*, **1**: 201-255; Mendoza.
- LEE, C.A. & SCHROTER, G.A. (1977): Memorial to ALEXANDER STOYANOW 1879-1974. – *Geological Society of America, Memorials*, **6**: 1-2.
- LEVY, R. (1969): Revision de las trigonias Argentina. Part 5. El grupo de las Pseudoquadrateae. – *Ameghiniana*, **6**: 65-68.
- LISSON, C.I. (1930): Contribución al conocimiento de algunas trigonias neocómicas del Perú. – *Boletín de Minas, Industrias y Construcciones*, (2), **20**: 3-26.
- LO FORTE, G.L. (1988): La fauna de trigonias (Mollusca, Bivalvia) del Tithoniano-Neocomiano de la Quebrada Blanca, Alta Cordillera de Mendoza. – 5to Congreso Geológico Chileno (Santiago de Chile), *Actas*, **2**: C277-293.
- LUCI, L. (2010): Encrusting patterns and life habit on Mesozoic trigonioids: a case study of *Steinmanella quintucoensis* (WEAVER) from the Early Cretaceous of Argentina. – *Lethaia*, **43**: 529-544.
- LUCI, L. & LAZO, D.G. (2012): The genus *Steinmanella* CRICKMAY (Bivalvia) in the transition between the Vaca Muerta and Mulichinco formations, Early Valanginian, Neuquén Basin, Argentina. – *Ameghiniana*, **49**: 96-117.
- LYCETT, J. (1872-1879): A monograph of the British fossil Trigoniae. – *Monographs of the Palaeontographical Society*, 1-245; London.
- MOROZUMI, Y., KUWANO, M., TANI, M., MIYAMOTO, J. & TASHIRO, M. (1981): Occurrence of *Steinmanella* (*Yeharella*) *japonica obsoleta* (Cretaceous trigonian) from the Izumi Mountains, southwest Japan, and its stratigraphic significance. – *Bulletins of the Osaka Museum of Natural History*, **34**: 1-5 [in Japanese].
- NAKANO, M. (1958): On some Upper Cretaceous *Steinmanella* (*Yeharella*) in Japan. – *Journal of Science, Hiroshima University, (C)*, **2** (2): 83-88.
- NAKANO, M. (1961): Note on *Steinmanella* (*Yeharella*) *ainuana* (YABE & NAGAO). – *Transactions and Proceedings of the Palaeontological Society of Japan, new series*, **44**: 139-145.
- NAKANO, M. (1968): On the Quadratotrigoniinae. – *Japanese Journal of Geology and Geography*, **39**: 27-41.
- OWEN, H.G. (1983): Atlas of continental displacement, 200 million years to present. – X + 159 pp.; Cambridge (University of Cambridge Press).
- PACKARD, E.L. (1921): The trigoniae from the Pacific coast of North America. – *University of Oregon Publications*, **1** (9): 1-35.
- PARKINSON, J. (1811): Organic remains of a former world. – London (Whittingham & Rowland).
- PÉREZ, E. & REYES, R. (1989): Catálogo analítico de los tipos de Trigoniidae (Mollusca – Bivalvia) descritos por R.A. PHILIPPI. – *Servicio Nacional Geológico Minero de Chile, Boletín*, **41**: 1-52.
- PÉREZ, E., REYES, R. & PÉREZ, V. (1981): Clave de las especies del género *Steinmanella* CRICKMAY, 1930 (Trigoniidae – Bivalvia). – *Revista Geológica de Chile*, **13-14**: 103-106.
- PHILIPPI, R.A. (1899): Los fósiles secundarios de Chile. Primera parte. – VI + 104 pp.; Santiago (Del Gobierno de Chile).
- POULTON, T. (1977): Early Cretaceous trigoniid bivalves of Manning Provincial Park, southwestern British Columbia. – *Geological Survey of Canada, Papers*, **76-9**: 1-25.
- RENNIE, J.V.L. (1936): Lower Cretaceous Lamellibranchia from northern Zululand. – *Annals of the South African Museum*, **31** (3): 277-391.
- REYES, R. (1970): La fauna de trigonias de Aisén. – *Boletín del Instituto de Investigaciones Geológicas*, **26**: 1-31.
- REYES, R. & PÉREZ, E. (1978): Las trigonias del Titoniano y Cretácico Inferior de la cuenca Andina de Chile y su valor cronoestratigráfico. – *Boletín del Instituto de Investigaciones Geológicas*, **32**: 1-105.
- REYES, R., PÉREZ, E. & SEREY, I. (1981): Estudios sistemático y filogenético de las especies sudamericanas del género *Steinmanella* (Trigoniidae – Bivalvia). – *Revista Geológica de Chile*, **12**: 25-47.
- RUDRA, P., BARDHAN, S. & SHOME, S. (2007): Phylogeny of the Late Jurassic-Early Cretaceous subgenus *Eselaevitrigonia* (Bivalvia) of Kutch, India, and palaeobiogeographic constraints. – *Journal of Paleontology*, **81** (5): 1066-1079.
- SAUL, L.R. (1978): The North Pacific Cretaceous trigoniid genus *Yaadia*. – *University of California Publications in Geological Sciences*, **119**: 1-65.
- SAUL, L.R. (1991): Type and referred specimens of fossil Invertebrata in the Natural History Museum of Los An-

- geles County: Mollusca formerly conserved at the University of California, Los Angeles. – iv + 72 pp.; Los Angeles (Los Angeles Museum).
- SAVEL'EV, A.A. (1958): The Lower Cretaceous trigoniids of Mangyschak and western Turkmenia. – Trudy Vsesoyuznogo Neftyanogo-Issledovatel'skogo Geologicheskikh Institut (VNIGRI), **125**: 1-516 [in Russian].
- SCOTT, R.W. (2007): Late Aptian – Early Albian bivalves of the Comanchean and Sonoran shelves. – *Bulletins of the New Mexico Museum of Natural History & Science*, **39**: 7-39.
- STEINMANN, G. (1881): Zur Kenntniss der Jura- und Kreideformation von Caracoles (Bolivia). – *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände*, **1**: 239-301.
- STEINMANN, G. (1882): Die Gruppe der Trigonidae Pseudoquadrateae. – *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilage-Bände*, **1**: 219-228.
- STOYANOW, A. (1949): Lower Cretaceous stratigraphy in southeastern Arizona. – *Geological Society of America, Memoirs*, **38**: 1-169.
- TASHIRO, M. (1978): On the occurrence of *Steinmanella* (*Yeharella*) *japonica obsolata* KOBAYASHI & AMANO, from Amakusa-Shimajima Island, Kyushu. – *Research Report, Kochi University, Natural Science*, **27**: 135-142.
- TASHIRO, M. (1988): Notes on “*Trigonia deckeina* KUBOTA” from the Cretaceous of Hokkaido. – *Memoirs of the Faculty of Science, Kochi University, (E)*, **9**: 11-14.
- TASHIRO, M. (1992): Illustrated book of fossils. Bivalves from the Mesozoic (Cretaceous) in Japan. – 308 pp.; Kumamoto (Shirono) [in Japanese].
- TASHIRO, M. & KANO, M. (1989): On a new species of *Yaadia* (Cretaceous trigonian) from Kyushu, Japan. – *Memoirs of the Faculty of Science, Kochi University, (E)*, **10**: 7-12.
- TASHIRO, M. & MOROZUMI, Y. (1982): Late Cretaceous knobby trigonians from the Izumi Mountains, southwest Japan. – *Bulletins of the Osaka Museum of Natural History*, **36**: 1-8.
- TOKUNUGA, S. & SHIMIZU, S. (1926): The Cretaceous formation of Futaba in Iwaki and its fossils. – *Journal of the Faculty of Science, Imperial University of Tokyo, (2)*, **1** (6): 181-212.
- TORRENS, H., BENAMY, E., DAESCHLER, E.B., SPAMER, E.E. & BOGAN, A.E. (2000): ETHELDRED BENETT of Wiltshire, the first lady geologist – her fossil collection in the Academy of Natural Sciences of Philadelphia, and the rediscovery of “lost” specimens of Jurassic Trigonidae (Mollusca: Bivalvia) with their soft anatomy preserved. – *Proceedings of the Academy of Natural Sciences*, **150**: 59-123.
- WEAVER, C.E. (1931): Paleontology of the Jurassic and Cretaceous of west central Argentina. – *Memoirs of the University of Washington*, **1**: 1-496.
- WHITEAVES, J.F. (1879): On the fossils of the Cretaceous rocks of Vancouver and adjacent islands in the Strait of Georgia. – *Geological Survey of Canada, Mesozoic fossils*, **1** (2): 93-190.
- YABE, H. & NAGAO, T. (1928): Cretaceous fossils from Hokkaido. Annelida, Gasteropoda and Lamellibranchiata. – *Science Report of the Tohoku Imperial University, Sendai, (2)*, **9**: 77-96.
- YEHARA, S. (1923a): Cretaceous trigonidae from Amakusa Islands, Higo Province, Kyushu, Japan. – *Journal of the Geological Society of Japan*, **30** (35): 1-12.
- YEHARA, S. (1923b): Cretaceous trigonidae from southwest Japan. – *Japanese Journal of Geology and Geography*, **2** (3): 59-84.

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