



THE GENERA *CALLIOTROPIS* SEGUENZA AND *AMBERCYCLUS* N. GEN. (VETIGASTROPODA, EUCYCLIDAE) FROM THE EARLY JURASSIC OF ARGENTINA

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ABSTRACT—The systematic position of the fossil species referred to *Calliotropis* is currently under debate due to the striking resemblance between these forms with their extant counterparts in general shell morphology and ornament pattern. We propose two temporal subgenera of *Calliotropis*: *Calliotropis* (*Riselloidea*) for Mesozoic species and *Calliotropis* (*Calliotropis*) for Cenozoic and Recent taxa. We also synonymize the families Eucyclidae and Calliotropidae, and redescribe the type genus of Eucyclidae based on topotypic material of *E. obeliscus* from Normandy. We argue that the generic name *Amberleya* should be restricted to its type species *Amberleya bathonica*. For the species that were traditionally included in *Amberleya*, we propose the new genus *Ambercyclus*, with its type species *Amberleya orbignyana*. The present paper also provides descriptions of three *Calliotropis* species from the Early Jurassic marine deposits of Argentina. The occurrence of *Calliotropis* (*Riselloidea*) *keideli* n. sp., *Calliotropis* (*Riselloidea*) cf. *C. (R.) keideli* and *Calliotropis* (*Riselloidea*) sp. in the Jurassic of Chubut and Neuquén provinces represents a new record of the genus in Early Jurassic sediments of Argentina and South America. Moreover, two species of *Ambercyclus* n. gen., such as *Ambercyclus espinosus* and *Ambercyclus? isabelensis* n. sp., are described from the same deposits. *Eucyclus*, *Amberleya*, *Ambercyclus*, and *Calliotropis* are included into Eucyclidae, which we consider to be a family of Seguenzioidea.

INTRODUCTION

CALLIOTROPIDS ARE a group of vetigastropods recently receiving an increase in attention from the malacologists due to their apparent morphological conservatism (e.g., Kano, 2008). Based on the living type species, *Calliotropis* (*Calliotropis*) *ottoi* (Philippi, 1844), the genus *Calliotropis* Seguenza, 1902 is mostly applied to the Cenozoic and modern forms, though Mesozoic taxa extraordinarily similar do exist already in the Jurassic (e.g., Kaim, 2004). This similarity was a reason for Hickman and McLean (1990) to include calliotropids into the mostly Mesozoic family Eucyclidae Koken, 1897. The antiquity of this entire group was confirmed by molecular investigations of Kano (2008) who found out that the calliotropids (=eucyclids) form an ancient lineage belonging to Seguenzioidea Verrill, 1884. The type genus of Eucyclidae is based on the Early Jurassic *Eucyclus obeliscus* Eudes-Deslongchamps, 1860 that has been a poorly known species, basically only from the original illustrations of Eudes-Deslongchamps (1860). Perhaps for this reason the genus was commonly synonymized with *Amberleya* Morris and Lycett, 1851 for which Cox and Arkell (1950) subsequently designated as type species the even worse known *Amberleya bathonica* Cox and Arkell, 1950 based on poorly preserved material. Recently topotypes of both species have been analyzed by one of us (Andrzej Kaim) in the collections of the Natural History Museum in London, U.K. Coincidentally, a new collection of Early Jurassic eucyclids has been assembled by the senior author from Argentina which gives us an opportunity to address the problem of eucyclid identity and the problem of *Eucyclus/Amberleya* synonymy or lack thereof.

HISTORICAL BACKGROUND

The family Eucyclidae Koken, 1897 is based on the genus *Eucyclus* Eudes-Deslongchamps, 1860 with the type species *E.*

obeliscus Eudes-Deslongchamps, 1860 from the Pliensbachian (Lower Jurassic) of Normandy, France, a species that is most closely similar to some living species of *Bathybembix* Crosse, 1893, e.g., *B. macdonaldi* (Dall, 1890). *Eucyclus* is commonly synonymized with *Amberleya* Morris and Lycett, 1851 though the type species of the latter is only remotely similar to *E. obeliscus* (see discussion below). There are also numerous Mesozoic eucyclid taxa very closely reminiscent of the extant genus *Calliotropis* Seguenza, 1902 and some authors (e.g., Kaim, 2004) included some Mesozoic species in this genus. Kaim (2004) observed that the only obvious difference between extant calliotropids and the Jurassic forms is the absence of umbilicus in the latter. Traditionally the Jurassic calliotropid-like species were grouped in the genus *Riselloidea* Cossmann, 1909. Kaim (2004) suggested that there are no serious taxonomic reasons to keep these Jurassic gastropods separate from Recent members of *Calliotropis*, and consequently synonymized both genera with *Riselloidea* being a junior synonym of *Calliotropis*. Kaim (2004) also pointed out that it is difficult to prove the biological relationships between Jurassic and modern forms but suggested keeping them together pending a more exhaustive revision on the fossil and living trochoids.

Nevertheless, Gründel (2007) retained *Riselloidea*, though he included it together with *Calliotropis*, *Biarmatoidella* Gründel (2003b) and *Trochonodus* Nützel et al. (2003) into the Calliotropinae of Hickman and McLean (1990). Later on, Gründel and Koppka (2007) classified two species of umbilicate Jurassic *Riselloidea*-like species in *Calliotropis*. Bandel (2010) also noted profound similarities between some species of modern *Calliotropis* and Jurassic *Riselloidea* but preferred to keep them separately.

The systematic position of *Calliotropis* was hotly debated during the last decade. Some authors included the genus in

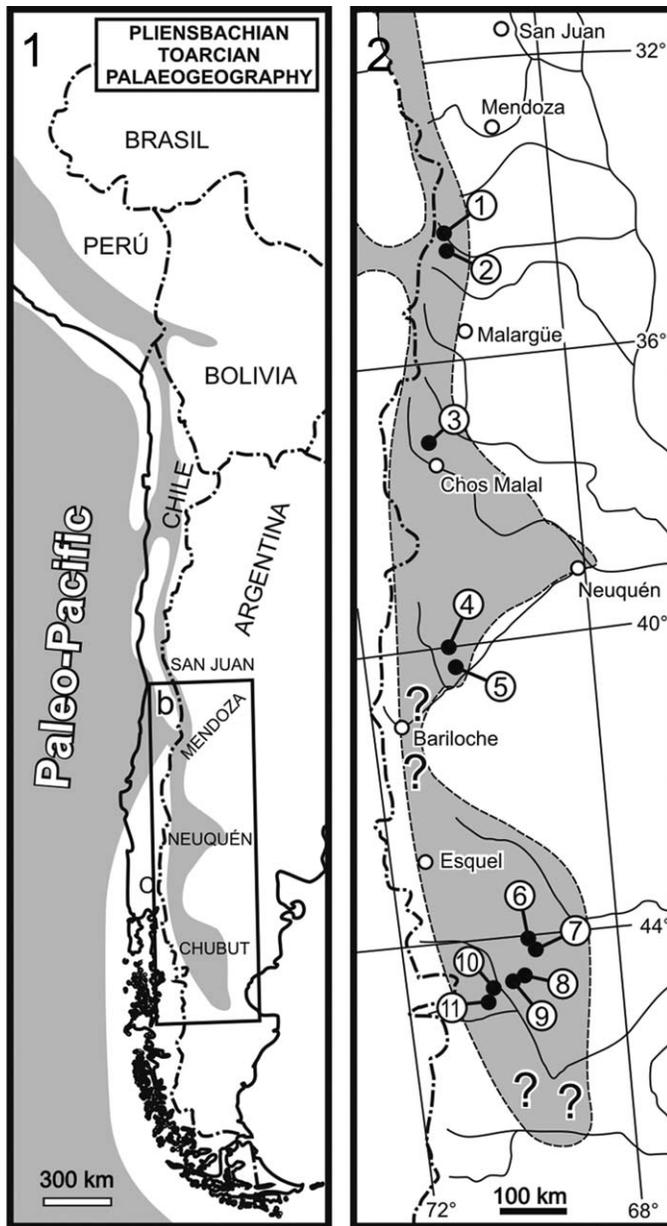


FIGURE 1—Location map and schematic stratigraphic sections with location of levels with eucyclid species described here. Fossiliferous localities mentioned in text, from North to South: 1, Portezuelo Ancho; 2, Cerro Tricolor; 3, Estación Rajapalo (Cordillera del Viento); 4, Estancia Santa Isabel; 5, Piedra Pintada; 6, Puesto Currumil; 7, Cañadón Puelman; 8, Betancourt; 9, Aguada Loca; 10, Lomas Occidentales; 11, Aguada Plate (modified of Vicente, 2005).

Calliotropinae, Chilodontidae (Bouchet and Rocroi, 2005; Vilvens, 2006, 2007; Poppe et al., 2006; Vilvens and Swinnen, 2008; Williams et al., 2008; Vilvens and Sellanes, 2010), while others assigned it to Calliotropini, Eucyclinae, Trochidae (Hickman and McLean, 1990; Kiel and Bandel, 2001; Vilvens, 2004; Kaim, 2004; Stilwell, 2005). Gründel (2000, 2007), and Gründel and Koppka (2007) included fossil members of *Calliotropis* in the Calliotropinae, Eucyclidae. Bandel (2010), based on anatomical features of living species, elevated Calliotropinae to the family level and included it in the superfamily Eucycloidea, a concept derived from Hickman and McLean (1990). Recent phylogenetic analyses based on

molecular data of Kano (2008) and Kano et al. (2009) suggest that extant species of *Calliotropis* are representatives of a monophyletic group to which he assigned family status, the Calliotropidae (superfamily Seguenzioidea). According to Kano (2008), living members of Seguenzioidea comprise the families Seguenziidae, Chilodontidae, Calliotropidae, and Cataegidae, while the Mesozoic Eucyclidae may represent an ancestral branch of the Seguenzioidea. However, the systematic relationships between the extinct Eucyclidae and the extant Calliotropidae remained unresolved.

ARGENTINEAN CALLIOTROPIDS

Although Pagani et al. (2012) and Ferrari (2013a) have recently reported some representatives of *Calliotropis* from the Jurassic of Argentina, Mesozoic members of this group are still very poorly known from South America. In the present research, three *Calliotropis*-like species are described from the Early Jurassic (Pliensbachian–Toarcian) marine sequences of the Chubut and Neuquén basins in Argentina (Fig. 1), namely *Calliotropis (Riselloidea) keideli* n. sp., *Calliotropis (Riselloidea)* cf. *C. (R.) keideli* and *Calliotropis (Riselloidea)* sp. Two members of the new genus *Ambercyclus*, *Ambercyclus espinosa* (Ferrari, 2009) and *Ambercyclus? isabelensis* n. sp., are also reported from the Chubut, Neuquén, and Mendoza provinces (Fig. 1).

The new eucyclid material of the Argentinean Jurassic provides a more complete data set of shell features useful to compare these faunas with coeval *Calliotropis* associations from other regions of the world, as well as with its modern representatives. Moreover, the occurrence of *Calliotropis* and *Ambercyclus* in the Jurassic of South America indicates for the first time a Gondwanan distribution of these genera at that time, and allows assessing possible paleobiogeographical connections between Tethyan and Antarctic seas. The updated morphologic and systematic data provided by the South American eucyclids are the necessary foundation to establish their phylogenetical relationships with the extant counterparts, which is crucial to get an appropriate interpretation of their evolutionary history.

The morphological descriptions follow Vilvens (2004, 2006, 2007) criteria, based on living *Calliotropis* species.

GEOLOGICAL SETTING

The Neuquén Basin (Fig. 1), which extended between S 34° and S 41°, is a Mesozoic back-arc basin on the western convergent margin of the South American plate (Legarreta and Gulisano, 1989), generated by extension linked to the fragmentation of Gondwana and the opening of the South Atlantic Ocean (Uliana and Biddle, 1988). Between S 34° and S 37°, it was restricted to a narrow N-S strip, but it broadened eastwards south of 37° to form the wide Neuquén embayment. It was filled with more than 6,000 m of marine and continental sedimentary and extrusive rocks of Late Triassic to Eocene age (Legarreta and Gulisano, 1989; Gulisano and Gutiérrez Pleimling, 1995). The basin originated from a series of unconnected, asymmetric, north-south oriented half grabens (Tankard et al., 1995), which controlled the subsidence and sedimentation during a first rifting in the Middle Triassic–Sinemurian (Ramos, 1992), when the non-marine and mainly non-fossiliferous siliciclastic and volcanic rocks filled the half grabens at the basin margins (Legarreta and Gulisano, 1989). Since Rhaetian times, the basin center was rapidly filled by nearshore sandstones and offshore shales, partly due to the Sinemurian–Toarcian regional sag phase (Vergani et al., 1995), which caused the half grabens to coalesce in the Pliensbachian (Legarreta and Gulisano, 1989), when the transgression widened. Features, areal distribution,

and age of the basal sag deposits depended on basement topography, controlled by the main faults and horsts, which also locally conditioned the beginning of the transgression and the partial synchronism between terrestrial and marine units of Late Triassic–Early Jurassic age (Gulisano, 1981; Gulisano and Gutiérrez Pleimling, 1995). In southern Mendoza Province the Pliensbachian–Toarcian sediments of the Atuel-western Malargüe depocenter which bear eucyclid species are referable to the Puesto Araya Formation, comprising Portezuelo Ancho (Fig. 1.1) and Cerro Tricolor (Fig. 1.2) localities. Eucyclids were also found in coeval deposits within the Neuquén embayment, at Estación Rajapalo (Fig. 1.3) in northern Neuquén in Cuyo Group beds, and in southern Neuquén in deposits of the Piedra Pintada Formation, cropping out at Estancia Santa Isabel (Fig. 1.4) and Piedra Pintada (Fig. 1.5) localities.

The Early Jurassic sediments in the Chubut province are distributed along a NW–SE belt of outcrops between S 42°30' and 44°30', and W 69°30' and W 71° (Riccardi, 1983; Giacosa and Márquez, 2000). In the Pampa de Agnia region, the Early Jurassic marine deposits of the Osta Arena Formation (Herbst, 1966; Nullo, 1983) reach a thickness of 190–340 m and the most extensive outcrops of this unit are exposed on the western slope of Sierras de Lonco Trapial, Cajón de Ginebra, and Cerro Negro. Part of the material here described was found on the western slope of Meseta de Catreleo, about two km north of Quebrada El Córdoba, at Puesto Currumil locality (Fig. 1.6; indicated as El Córdoba in Ferrari, 2009) (Ferrari 2012, 2013a; Pagani et al., 2012). Further south from the Puesto Currumil locality, the marine sequence of Osta Arena Formation also yields eucyclid species, and is exposed at Cañadón Puelman (Fig. 1.7) locality. In the southwestern region of the Chubut Province, the Early Jurassic marine deposits crop out in Ferraroti and Nueva Lubecka areas, and they are known as Mulanguñeu Formation (Fernández Garrasino, 1977). The most extensive deposits of this unit crop out on the western slope of Salar de Ferraroti and Lomas Occidentales near the Rio Genoa valley. Most of the eucyclid material here described comes from Aguada Loca (Fig. 1.9), Lomas Occidentales (Fig. 1.10), Aguada Plate (Fig. 1.11), and Lomas de Betancourt (Fig. 1.8) localities, situated east and west of the old telegraphic station of Nueva Lubecka.

MATERIAL AND METHODS

The present material was collected by M. Ferrari, S. Damborenea, and M. Manceñido during different campaigns in several fossiliferous localities (Fig. 1). Some of them (Lomas Occidentales, Aguada Plate, Aguada Loca, Lomas de Betancourt, Puesto Currumil and Cañadón Puelman) are located in west central Chubut Province. Others are situated in Mendoza and southern Neuquén provinces, namely Portezuelo Ancho, Cerro Tricolor, Arroyo Lepa, Estación Rajapalo, Estancia Santa Isabel and Piedra Pintada localities. The stratigraphical sections were described in Damborenea (1987, figs. 3–5), Pagani et al. (2011, fig. 1c), Pagani et al. (2012, fig. 1b), and Ferrari (2013, fig. 1, 2014, fig. 1). The accompanying fauna is abundant and very diverse, comprising mostly epifaunal bivalves, brachiopods, ammonites, other gastropods, and corals. All of the material was found in late Pliensbachian (*Fanninoceras* Zone)/early Toarcian (*Dactyloceras* Zone) beds, according to the current ammonite biozonation (Riccardi, 2008a, 2008b; Riccardi et al., 2011).

The Argentinean eucyclid material is stored in the Museo Paleontológico Egidio Feruglio collection (MPEF), Trelew, and in the División Paleozoología Invertebrados, Museo de Ciencias Naturales de La Plata (MLP) collection, La Plata. All specimens

were prepared by technical staff of the MPEF laboratory (Leandro Canessa and Santiago Bessone) and latex casts were prepared from specimens preserved as external molds. The specimens were coated with ammonium chloride to enhance sculpture details for photography. Photographs were taken by digital camera with binocular lens at MPEF, and by scanning electronic microscopy (SEM) at ALUAR (Pto. Madryn).

Institutional abbreviations.—MLP, Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina; NHMUK, Natural History Museum, London, U.K.; ALUAR, Aluminio Argentino, Pto. Madryn, Chubut, Argentina.

Morphological abbreviations.—H, Height; W, Width; H/W, Height/Width ratio.

SYSTEMATIC PALEONTOLOGY

Class GASTROPODA Cuvier, 1795

Subclass ORTHOGASTROPODA Ponder and Lindberg, 1997

Order VETIGASTROPODA Salvini-Plawen, 1980

Superfamily SEGUENZOIDEA Verrill, 1884

Family EUCYCLIDAE Koken, 1897

Genus EUCYCLUS Eudes-Deslongchamps, 1860

Type species.—*Eucyclus obeliscus* Eudes-Deslongchamps (1860) from the Pliensbachian of Normandy, France.

Diagnosis.—Emended: shell low turriculate to high trochiform, whorls characterised by a strong keel near the abapical suture, which produces angulation of the flank. Flank ornamented by spiral cords bearing usually small beads.

Remarks.—The designation of the type species by Eudes-Deslongchamps (1860, p. 141) is very clear and it is surprising that this matter was debated over years. It resulted perhaps from the statement of Wenz (1938, p. 264) who erroneously considered *Turbo ornatus* Sowerby (1819) (from the Middle Jurassic of England) to be the type species. *Eucyclus obeliscus* Eudes-Deslongchamps (1860) is a junior synonym of *Turbo julia* d'Orbigny (1853) which is based on material of the same age and locality (compare Fischer and Weber, 1997, pl. 21, fig. 11).

In the original diagnosis, Eudes-Deslongchamps (1860, p. 141) described members of *Eucyclus* as “Coquille spiralee, ovale-oblongue, pyramidale, ou presque turriculee, à tours arrondis, croissant régulièrement, à suture enfoncée. Surface des tours couverte de plis transversaux plus ou moins nombreux, plus ou moins saillants, tranchants ou granuleux, et meme dentés; souvent un ou plusieurs de ces plis, plus développés, forment sur la partie visible des tours une ou plusieurs carènes. De petits plis longitudinaux ou obliques, très-nombreux, souvent ondulés et bifurqués, comme anastomosés, coupent les plis transversaux et rappellent par leur aspect ceux qui se voient sur plusieurs Littorines vivantes et sur les espèces du genre *Onustus*, notamment *l'O. indicus* (*Trochus indicus* L.). Base oblique, plus ou moins arrondie, avec plis concentriques, plus ou moins nombreux, coupés par de nombreux petits plis ou stries rayonnantes. Point d'ombilic. Bouche ovale, rétrécie et anguleuse en haut. Lèvre droite demi-circulaire, mince, tranchante, comme gaufrée par l'origine des plis transversaux; lèvre gauche non apparent sur le retour de la spire; mais en s'appuyant sur la columelle, elle s'épaissit et s'élargit de manière à former une surface assez étendue, plane ou arrondie. En s'unissant à la lèvre droite, elle forme un coude prononcé plus ou moins ouvert; mains sans qu'il y ait d'échancre à l'union des deux lèvres”. Subsequently, Blake (1905, p. 83) emended the genus's diagnosis as follows: Pyramidate, or nearly turriculate. Shell very thin; whorls rounded, increasing regularly; suture imbedded; surface covered with various transverse [spiral] folds, non-umbilicated; mouth oval, right lip semicircular, thin; left lip not seen on the return of the

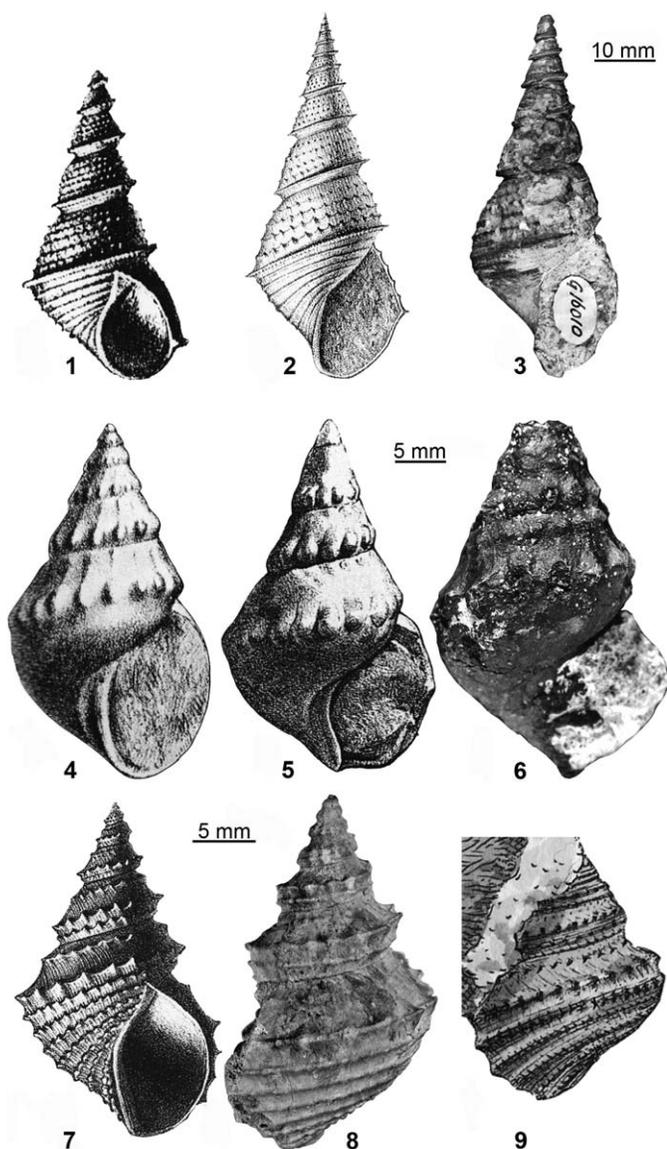


FIGURE 2—Fossil eucyloid genera and their type species. 1, *Eucyclus julia* (d'Orbigny 1853); the senior synonym of *E. obeliscus*, type species of *Eucyclus*; original illustration from d'Orbigny (1851–1860: pl. 328, fig. 3); 2, 3, *Eucyclus obeliscus* Eudes-Deslongchamps, 1860: 2, original drawing from Eudes-Deslongchamps (1860 pl. 11, fig. 9); 3, topotype NMHUK PI G.16010 from Pliensbachian of Fontaine-Étoupefour, Normandy, France; 4, 6, *Amberleya bathonica* Cox and Arkell, 1950, type species of *Amberleya*; 4, “*Amberleya (Pagodus) nodosa* (Buckman, 1845)” sensu Morris and Lycett (1851, pl. 5, fig. 19) (nomen dubium) replaced by *Amberleya bathonica* Cox and Arkell, 1950; 5, the same species illustrated in Knight et al. (1960, fig. 203.5); 6, NHMUK PI MG1464, specimen from the Bathonian of England; 7–9, *Ambercyclus orbignyana* (Hudleston 1892), type species of *Ambercyclus*: 7, *Purpurina ornata* (Sowerby 1819) sensu d'Orbigny (1853, pl. 330, fig. 4), replaced by *Amberleya orbignyana* Hudleston, 1892; 8, NHMUK PI G.92262 from “Oolite inferieur” of St. Vigor near Bayeux, Normandy, France; 9, *Ambercyclus ornatus* (Sowerby, 1819), original drawing from Sowerby (1819, tab. 240.2).

spire, but resting on the columella, which it thickens and enlarges, unites at a more or less open angle, but makes no notch with the right lip.

We are proposing here a new emended diagnosis of *Eucyclus* based on topotypic material housed at the Natural History Museum in London (see above).

In contrast to *Eucyclus*, *Amberleya* (see below) has clearly two broad spirals armoured with large and blunt nodes. In *Amberleya*,

each node of the abapical spiral is paired with single node of adapical spiral by interconnecting wide and blunt axial rib while tiny nodes of *Eucyclus* are arranged in spirals without clear axials between them. Moreover the base of *Eucyclus* is ornamented by numerous spiral ribs, while in *Amberleya bathonica* no such feature can be observed (Fig. 2). Very similar is *Eucyclomphalus* von Ammon, 1892, which differs in having a wide umbilicus. The same concerns the genus *Trypanotrochus* Cossmann, 1918, which is very similar to *Eucyclus* but possesses a clear though narrow umbilicus. Here we should perhaps express our doubts as to whether presence/absence of the umbilicus is indeed of generic importance in this group. In any case all three genera are closely related.

As rightly stated already by Blake (1905, p. 83), a large number of Jurassic species corresponds to the concept of *Eucyclus* as diagnosed by Eudes-Deslongchamps (1860). This and the confusion as for the type species of *Eucyclus* resulted in an extensive discussion on the identity of the genus and its possible synonymy with *Amberleya* Morris and Lycett, 1851 (see below). Here we re-illustrate the original figure, the type species of Eudes-Deslongchamps (1860, pl. 11, fig. 9), the original figure of synonymous *Eucyclus julia* (d'Orbigny, 1853, pl. 328, figs. 3, 4.), and topotypic material of *Eucyclus obeliscus* housed at the Natural History Museum in London (Fig. 2). We propose to restrict the usage of the generic name *Eucyclus* to non-umbilicate shells possessing a single strong keel near the abapical suture.

Genus AMBERLEYA Morris and Lycett, 1851

Type species.—“*Terebra nodosa* Buckman, 1845” sensu Morris and Lycett (1851) (nomen dubium) replaced by *Amberleya bathonica* Cox and Arkell, 1950 (see also Knight et al., 1960). Great Oolite, Bathonian, England.

Diagnosis.—Emended: shell with small umbilicus, a single abapical keel plus an adapical spiral cord, ornament consisting on blunt nodes, and smooth shell base.

Remarks.—In the original diagnosis, Morris and Lycett (1851, p. 54) grouped members of *Amberleya* as “shell turreted, turbinated, apex acute; whorls flattened above, convex and nodulated beneath, the last whorl ventricose; aperture ovate, entire; inner lip thickened, and nearly covering a small umbilicus; sutures deeply impressed; no columella”.

Golikov and Starobogatov (1975) clearly established the distinction between *Eucyclus* and *Amberleya*, and more recently, several authors followed also this interpretation (e.g., Szabo, 1995; Conti and Monari, 2001; Grundel, 2007). As outlined above, type species of both genera differ significantly and we propose herein to treat them as separate taxa. We propose to restrict the usage of the name *Amberleya* to shells with small umbilicus, a single abapical keel plus an adapical spiral cord, ornamented by blunt nodes and smooth shell base. This would restrict it largely to the type species *A. bathonica* (Fig. 2). For the taxa commonly identified as *Amberleya* (i.e., bicarinate shells with pointed nodes and ornamented base) we propose the new genus *Ambercyclus* below.

AMBERCYCLUS new genus

Type species.—*Amberleya orbignyana* Hudleston, 1892 (= *Purpurina ornata* d'Orbigny, 1850; preoccupied), from the Middle Jurassic (Bajocian) of England.

Other species.—*Turbo capitaneus* Münster, 1844, *Amberleya decorata* Martin, 1858, *Turbo elegans* Münster, 1844, *Turbo ornatus* Sowerby, 1819, *Amberleya pagodiformis* Hudleston, 1892, *Amberleya obornensis* Hudleston, 1892, *Eucyclus goniatus* Eudes-Deslongchamps, 1860, *Turbo purchisoni* Münster, 1844, *Trochus bisertus* Phillips, 1829, *Amberleya generalis* Münster, 1844, *Amberleya armigera* Lycett, 1863, *Amberleya monilifera*

Lycett, 1863, *Amberleya dilleri* Stanton, 1895, *Turbo morganensis* Stanton, 1895, *Trochus gaudrianus* d'Orbigny, 1852, *Amberleya? espinosa* Ferrari, 2009, and probably also *Ambercyclus? isabelensis* n. sp.

Diagnosis.—Shell trochiform, distinctly conical to slightly pagodiform; with a small umbilicus; juvenile whorls convex, mature whorls characterized by a strong peripheral spiral keel with pointed nodes; weaker spiral keel with small nodes located below the peripheral keel; a third spiral keel near the adapical suture; fine prosocline collabral ribs connecting nodes of spiral elements. Sutures incised in a fine spiral furrow. Base strongly convex with regularly spaced spiral cords, with or without nodes. Aperture oval; inner lip thickened forming a concave callus; outer lip thin and indented by peripheral spiral cord (Fig. 2).

Etymology.—Referred to the eucyclid forms having morphological characters intermediate between *Amberleya* and *Eucyclus*.

Occurrence.—Early Jurassic (Pliensbachian–Toarcian), Argentina; Middle Jurassic (Bajocian)—Early Cretaceous, Europe and United States.

Remarks.—The fossil representatives of the new genus *Ambercyclus* are very similar in general shell morphology and ornament pattern with the extant calliotropinids *Bathybembix* Crosse (1893), *Lischkeia* Fischer in Kiener and Fischer (1879), and *Ginebis* Taki and Otuka (1943). Members of *Bathybembix* show a pagodiform shell shape bearing a peripheral spiral keel with pointed nodes, and a smaller spiral keel with weaker nodes near the adapical suture.

Fine prosocline growth lines connect the nodes of both keels. The base is strongly convex ornamented with nodose spiral cords. *Bathybembix* differs from *Ambercyclus* in having more convex teleoconch whorls, a strongly circular aperture, and the peristome is not indented by peripheral spiral cord. According to Bandel (2010, p. 474), representatives of *Bathybembix* have a conical shell with a keel above the suture, flat upper whorls and triangular-section groove at the suture, a rounded base with spiral ribs and the umbilicus is closed in adults. The species of *Bathybembix* are known from the fossil record at least from the late Eocene (Hickman and McLean, 1990). In the Paleogene and Neogene they underwent a radiation in bathyal depths of the north Pacific rim. *Bathybembix* is now richly represented from the Japan to the Americas, in bathyal (>200) to abyssal depths apparently adapted to cold waters with a bipolar distribution (Hickman and McLean, 1990). *Bathybembix aeola* (Watson, 1879), *Bathybembix macdonaldi* (Dall, 1890), *Bathybembix bairdii* (Dall, 1889) are typical representatives of this genus. *Ginebis*, commonly considered as a subgenus of *Bathybembix*, is also very similar to the fossil genus *Ambercyclus* in shell shape, but differs in having less developed nodular and collabral elements, and slightly more convex teleoconch whorls. The type species *Ginebis argenteonitens* (Lischke, 1872) is frequently found offshore Japan and Taiwan. The extant members of *Lischkeia* resemble the extinct *Ambercyclus*; however, they have the inner lip forming a rounded callus with a central groove, and have a slightly thickened outer lip (Bandel, 2010, p. 464). The species of *Lischkeia* live in deep waters and are frequently found in bathyal depths (>100 m); they are commonly distributed in the Pacific Ocean from the Philippine Islands to Japan (Poppe et al., 2006). *Lischkeia alwiniae* (Lischke, 1871), *L. undosa* Kuroda and Kawamura, 1956, *L. reginamaris* Habe and Okutani, 1981, *L. imperialis* (Dall, 1881) are representatives of this genus. The similarities of these deep-water taxa to the extinct tropical, shallow-water eucyclinids have been discussed in Hickman and McLean (1990) and Kano (2008).

Fossil representatives of *Calliotropis (Riselloidea)* (see below) are also very similar to the new genus *Ambercyclus* in general shell morphology and ornament pattern, with the typical

interruption of primary axial ribs towards the mature teleoconch whorls (Jaitly et al., 2000). *Calliotropis (Riselloidea)* members, however, have a less conical and more gradate shell shape with a slightly lower spire. They have also a first teleoconch whorl smooth and convex, while in *Ambercyclus* these characters are unknown. *Calliotropis (Riselloidea)* members are also smaller, have more rounded and less pointed nodes on the peripheral spiral keel, and lack the third abapical spiral cord just below the peripheral spiral keel. *Ambercyclus* shows also close resemblance to *Eucycloscala*, in general shell morphology and ornament pattern. However, *Eucycloscala* Cossmann, 1895 has strongly convex juvenile teleoconch whorls, more distinct axial ribs on the shell surface, less acute nodes, an aperture circular and a peristome continuous (see diagnosis Bandel, 2010).

AMBERCYCLUS ESPINOSUS (Ferrari, 2009)

Figure 3.1

2009 *Amberleya? espinosa* Ferrari, p. 450, fig. 2A.

Diagnosis.—Emended: anomphalous, conical to slightly coeloconical shell; axial ribs developed on the first four teleoconch whorl; on last teleoconch whorl, the abapical spiral keel much stronger than the adapical one, with acute, widely spaced and spinose nodes; a third spiral keel with small and rounded nodes appears at abapical suture on fourth teleoconch whorl; sutures impressed; base slightly convex with three nodular spiral cords, the innermost with more developed nodes.

Description.—The material originally described and figured by Ferrari (2009, p. 450, fig. 2A) presents a shell of medium size with a height of 20.6 mm and a width of 16.8 mm; height of the shell is 1.2–2.4 times the width; apical angle of 77°; without umbilicus.

Protoconch is not preserved. Teleoconch comprises up to seven whorls, the surface of the whorls is slightly concave becoming flat and angular near the periphery; the outer face is vertical. The teleoconch whorls bear three spirals and strongly spinose keels, and collabral ribs on the shell surface. The axial elements are well developed on the early teleoconch whorls and become weaker during ontogeny; nodes on cords are spinose and placed at the intersection with axial elements. Suture impressed.

The first teleoconch whorl is convex, and axial ribs are not clearly visible. On the second teleoconch whorl primary spiral cords are developed with rounded nodes; six visible, thick and slightly prosocline axial ribs are present. On the third teleoconch whorl, the peripheral spiral keel is still stronger and with more acute nodes than the sutural cord. On fourth and fifth teleoconch whorls, axial ribs are weaker and nodes on the peripheral keel stronger, spinose and acute; a third abapical spiral cord with small and rounded nodes appears at suture. On last whorl, the peripheral keel with strongly spinose nodes; the sutural cord weak with small and separate nodes; the third abapical spiral keel bordering the base, weak and with slightly developed nodes; axial ribs connecting the primary spiral elements become obsolete; fine prosocline growth lines appear on last teleoconch whorl.

The base is slightly convex and ornamented by three conspicuous and nodular spiral ribs; the innermost has stronger and rounded nodes. The aperture is incompletely preserved but a narrow and straight columellar lip is present.

Types.—Holotype, MPEF-PI 1882; paratype, MPEF-PI 1874 (see Ferrari, 2009).

Occurrence.—PA-06 site from Puesto Currumul fossiliferous locality, Early Jurassic (early Toarcian) of Osta Arena Formation, Chubut Province, Argentina.

Remarks.—The specimens here described were originally assigned doubtfully to the genus *Amberleya* (see Ferrari, 2009). We propose here to emend the diagnosis of the species (see above).

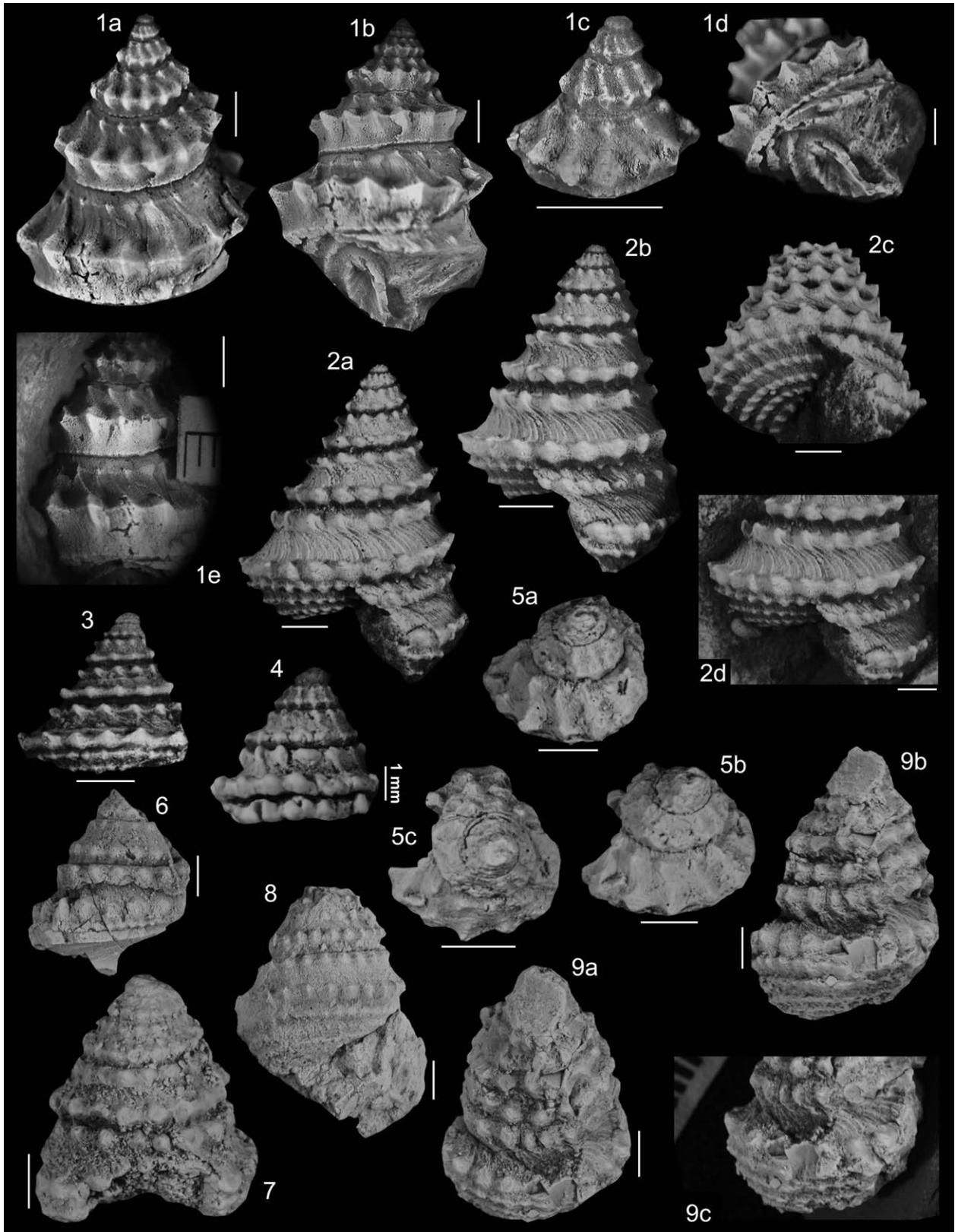


FIGURE 3—1, *Ambercyclus espinosus* (Ferrari, 2009). MPEF-PI 1882, holotype; 1a, 1b, adult teleoconch in lateral view; 1c, juvenile teleoconch in lateral view; 1d, last teleoconch whorl in basal and apertural views; 1e, sutural detail; 2–9, *Ambercyclus? isabelensis* n. sp.: 2, MLP 18822, holotype; 2a, 2b, adult teleoconch in lateral view; 2c, basal and apertural detail; 2d, outer face ornament detail; 3, MLP 18823, juvenile teleoconch in lateral view; 4, MPEF-PI 4165, juvenile teleoconch in lateral view; 5, MPEF-PI 3579-3; 5a, 5b, juvenile teleoconch in lateral view; 5c, juvenile teleoconch in apical view; 6, MPEF-PI 3579-6, fragment specimen in lateral view; 7, MPEF-PI 3579-5, adult teleoconch in lateral view; 8, MLP 18828, paratype, adult teleoconch in lateral view; 9, MPEF-PI 3579-8; 9a, 9b, adult teleoconch in lateral view; 9c, ornament detail. Scale bars=3 mm except where otherwise noted.

TABLE 1—Dimensions (mm) of *Ambercyclus? isabelensis* n. sp. Asterisk indicates missing data.

<i>Ambercyclus? isabelensis</i> n. sp.	Type	Height	Width	Apical angle
MLP 12165		12.6	11.7	*
MLP 18822	Holotype	20.4	15.3	77°
MLP 18823		8.5	8.2	64°
MLP 18826		15.7	12	*
MLP 18827-1		16.7	14.7	*
MLP 18827-2		14.8	12.8	*
MLP 18827-3		13.3	11.2	*
MLP 18827-4		18.5	13.8	*
MLP 18828	Paratype	19.7	16.2	*
MPEF-PI 3579-1		6.5	8.7	*
MPEF-PI 3579-2		7.9	7.6	*
MPEF-PI 3579-3		8	8.7	81°
MPEF-PI 3579-4		9.7	8.1	*
MPEF-PI 3579-5		12.7	11.5	*
MPEF-PI 3579-6		13.3	12.8	*
MPEF-PI 3579-7		14.3	12.8	*
MPEF-PI 3579-8		19.1	13.2	*
MPEF-PI 4165	Paratype	3.3	2.7	71°

Ambercyclus espinosus (Ferrari, 2009) is very similar to the type species *Ambercyclus orbignyanus* (Hudleston, 1892), from the Middle Jurassic (Bajocian) of England. Both have spinose nodes on peripheral spiral keel; but in the European form these are slightly weaker. Moreover *A. orbignyanus* has two equally developed peripheral spiral keels, a more elongated spire and narrower apical angle of 45°. The species here described resembles *A. goniatus* (Eudes-Deslongchamps, 1860) (Hudleston, 1892, p. 284, pl. 22, fig. 6), from the Middle Jurassic of England. The latter species was erected upon a juvenile specimen with an acute spire, obtuse apical angle, marked gradate shell shape and smaller and less pointed nodes than in *A. espinosus*. *Ambercyclus espinosus* is also comparable to *Ambercyclus capitaneus* (Münster, 1844) (Hudleston, 1892, p. 277, pl. 21, fig. 12; Szabó, 1982, p. 24, pl. 3, figs. 1, 2; Fisher and Weber, 1997, p. 135, pl. 21, fig. 12a, 12b), from the late Early and early Middle Jurassic (Toarcian–Aalenian) of Europe. The latter, however, has smaller and less pointed nodes, two equally developed peripheral spiral keels on the teleoconch whorls, a third abapical keel appearing on last whorl, more developed spiral and collabral elements on the shell surface, and a more convex base. *Ambercyclus capitaneus* has been described in detail by Schulbert and Nützel (2013, p. 731) who argue that the characteristic ornament of axial threads which are opisthocyrt between the spiral keels is unusual for the genus *Eucyclus*. It is also unusual for *Ambercyclus* though we feel it is a better place for the species than *Eucyclus* pending further research. *Ambercyclus obornensis* (Hudleston) (1892, p. 286, pl. 22, fig. 10), from the Middle Jurassic of England, represents one of the most elongated forms of the genus and, thus, differs from *A. espinosus* in being higher, with a more pointed spire and a narrower apex of 40°. *Ambercyclus obornensis* has also smaller and more separated nodes than *A. espinosus*, and a more elongated columellar lip in the juvenile specimens.

AMBERCYCLUS? ISABELENSIS new species

Figure 3.2–3.9

2011 *Calliotropis* cf. *keideli* Ferrari, p. 64, pl. 4, figs. 12, 13.

Diagnosis.—Shell anomphalous, distinctly conical, slightly pagodiform to trochiform, with peripheral keel; first teleoconch whorl convex and smooth. Adult teleoconch whorls strongly spinose with well developed prosocline and opisthocyrt axial riblets; a third spiral keel with acute nodes bordering the base on last whorl; base moderately convex, with four nodular spiral cords, the innermost with stronger nodes. Aperture not completely visible; columellar lip thickened.

Description.—Dextral, trochiform, conical to slightly pagodiform and high-spined shell, without umbilicus. Shell rather acute, with a height up to 20.4 mm and a width up to 15.3 mm, height of the shell is 1–1.3 times the width, and three times the aperture height; apical angle varies from 64° to 81°.

Protoconch unknown. Teleoconch up to seven whorls, the surface of the whorls is flat to slightly concave. The teleoconch bears three primary spiral and nodular cords and axial ribs on the shell surface; nodes are placed at the intersections of cords with axial elements on the three first whorls. Suture well distinct, impressed and canaliculated.

First teleoconch whorl convex and smooth. On second teleoconch whorl, two spiral cords are equally developed, with acute nodes on the peripheral keel and rounded nodes on the sutural cord; primary axial ribs orthocline and distinct, connecting nodes on primary spiral cords. On third teleoconch whorl, the peripheral keel stronger and with more acute nodes than the sutural cord; axial ribs still present but less developed. On fourth whorl, nodes on the spiral elements strongly acute and spinose, but still slightly more developed on the peripheral keel; primary axial ribs become obsolete, and secondary prosocline and opisthocyrt axial threads appear on the outer face; a third abapical spiral cord appears weakly at suture. At the beginning of fifth whorl, a weak sutural ramp is developed. On fifth teleoconch whorl, nodes on the peripheral spiral keel still acute and stronger than on the sutural cord; the third spiral keel completely visible at suture, with separate, rounded and small nodes. On sixth whorl, the peripheral and sutural cords equally developed, and acute nodes oriented adapically; secondary axial ribs more developed on the outer face; nodes on the third keel stronger. On last teleoconch whorl, the sutural cord weaker than the peripheral keel; the third cord located abapically; secondary axial ribs still visible.

Base moderately convex, with four strongly nodular spiral cords; the innermost slightly more developed than the outermost and with stronger nodes. The spiral cords intercept fine, orthocline to slightly prosocline, crowded collabral ribs. The aperture is not clearly visible, and the columellar lip thickened. Dimensions (mm) given in Table 1.

Etymology.—Referred to Estancia Santa Isabel (Neuquén Province), where the type material was found.

Types.—Holotype, MLP 18822; paratypes, MLP 18828 and MPEF-PI 4165. Two specimens preserved as external molds.

Other material.—MLP 12165, 18823–18827 and MPEF-PI 3579. Six specimens preserved as external molds.

Occurrence.—Beds 1,049 and 1,052 at Santa Isabel (late Pliensbachian–early Toarcian); bed 805 at Cerro Tricolor (early Toarcian); beds 1,286 and 1,287 at Portezuelo Ancho (late Pliensbachian), Piedra Pintada Formation, Neuquén Province, Argentina. Bed PA 06 from Puesto Currumil locality, Early Jurassic (early Toarcian), Osta Arena Formation; bed LO 29 from Lomas Occidentales locality, Early Jurassic (late Pliensbachian–early Toarcian), Mulanguíñeu Formation, Chubut Province, Argentina.

Remarks.—The species here described most probably represents a member of *Ambercyclus* (see diagnosis above). However, the new species here proposed has a high conical and trochiform shell, and is slightly gradate to pagodiform. Moreover, the whorls of *Ambercyclus? isabelensis* n. sp. are flat to concave, and lacks the third abapical peripheral spiral cord on most specimens; thus the species is here tentatively assigned to *Ambercyclus*.

Ambercyclus? isabelensis differs from *A. espinosus* (Ferrari) in having a less angular and more conical shell shape; stronger secondary axial ribs on the whorl surface; more acute and crowded spinose nodes on peripheral spiral keel, oriented adapically; and a moderately convex base.

Genus CALLIOTROPIS Seguenza, 1902

Type species.—*Trochus ottoi* Philippi (1844) by monotypy; Pleistocene of Sicily, Italy. This species has been recognized as a still living member of *Calliotropis* in the Mediterranean Sea and in the eastern and northern Atlantic Ocean (e.g., Kaim, 2004; Bandel, 2010).

Occurrence.—Upper Triassic–Middle Jurassic of Europe, India and South America; Upper Cretaceous of Europe; Eocene of Antarctica; cosmopolitan during Holocene.

Remarks.—The high interspecific variability in form (tall to depressed), adult size sculpture and umbilical development have been considered as the most meaningful characters of *Calliotropis* (Marshall, 1979; Dell, 1990; Stilwell, 2005; Vilvens, 2007). Stilwell (2005), however, argued that the recognition of species assigned to *Calliotropis* based only on shell characters, would be fruitless, especially given the geographically and temporally disjunct distribution in the fossil record. The author reported the first fossil *Calliotropis* (*Calliotropis*) *antarchais* Stilwell (2005) in the Eocene of Antarctica and considered his species as a basal member of the group, suggesting that the strongly and coarsely reticulate shell sculpture retained throughout the ontogeny in this species is much reduced on most teleoconch whorls of most extant forms. Moreover, Stilwell (2005) suggested that the shallow-water habitat of *C. (C.) antarchais* seems to be a basal condition of the group, comparing the frequent occurrence of living calliotropids in bathyal depths environments.

In the present paper, the Jurassic species closely recollecting *Calliotropis* are accommodated in a temporal subgenus *Riselloidea* (previously considered to be a full genus). *Biarmatoidella* shows extremely resemblance to *Riselloidea*, although it has a columellar callus with a thickening. *Trochonodus* might be another temporal subgenus of *Calliotropis*, pending more detailed investigation on type species of both subgenera.

Subgenus RISELLOIDEA Cossmann, 1909

Type species.—*Risellopsis subdisjuncta* Cossmann (1909). Jurassic of northern France, by monotypy.

Remarks.—Kaim (2004) pointed out that the only difference between extant members of *Calliotropis* and the Jurassic forms is the absence of an umbilicus in the latter, however, the absence/presence of umbilicus seems to be an unstable character. Another difference is the larger and bulbous protoconch of modern *Calliotropis* while it is much smaller and depressed in Jurassic species (see e.g., Kaim, 2004, p. 23, fig. 9). Bandel (2010, p. 458) stated that *Riselloidea* is distinct from *Calliotropis* though giving no grounds for that opinion apart from considerable difference in geological age (175 Ma) and placed both genera in two different families (Eucyclidae vs. Calliotropidae).

Here, we consider that there are no serious taxonomic reasons to keep the extant *Calliotropis* separately from the Jurassic *Riselloidea*, however, taking into account the great and disjunct temporal distance between both forms we decided preserve *Riselloidea* as a temporal subgenus of *Calliotropis*.

CALLIOTROPIS (RISELLOIDEA) KEIDELI new species
Figures 4.1–4.13, 5.1–5.8

2011 *Calliotropis keideli* Ferrari, p. 56, pls. 2–4.

2012 *Calliotropis* sp. Pagani et al., p. 414, fig. 4j.

Diagnosis.—Shell pseudumbilicated, pagodiform, conical to slightly coeloconical, with peripheral keel; first teleoconch whorl smooth and convex; second teleoconch whorl convex with axial ribs. Adult teleoconch whorls strongly gradate, nodular with poorly developed axial ornament; base convex, with four spiral cords, the innermost nodular bordering the umbilical area. Aperture holostomatous and subcircular.

Description.—Dextral, pagodiform, conical to slightly coeloconoidal and high-spired shell. Shell rather small for the genus,

with a height up to 15.7 mm and a width up to 9.2 mm, height of the shell is 1–1.8 times the width, and 2.2–2.5 times the aperture height; apical angle ranges from 71° to 85°; pseudumbilicus present in some specimens.

Protoconch unknown. First teleoconch whorl consists of one convex, depressed and smooth whorl of about 600 µm–1 mm height, and 700 µm–1.6 mm width. Teleoconch up to six whorls, the outer face of the whorls is slightly concave becoming flat and vertical abapically. The teleoconch bears three primary spiral and nodular cords and axial ribs on the shell surface; nodes on cords are produced by the intersection with axial elements on the three first whorls. Suture impressed.

Second teleoconch whorl convex, sculptured with 14–15 regularly spaced axial ribs, slightly prosocline and smooth; interspaces between ribs two times broader than ribs; the peripheral spiral keel appears almost immediately. On second teleoconch whorl, two primary spiral keels distinct; the peripheral keel slightly stronger than the sutural cord, both with nodes at the intersection point with axial ribs; nodes are small and rounded, and stronger on the peripheral keel; axial ribs more developed and prosocline than on first whorl. On third whorl, a third abapical spiral cord emerging weakly from suture; the peripheral keel still stronger than the sutural cord; nodes rounded to slightly acute; axial ribs become obsolete. On fourth and fifth whorls, a third spiral keel visible, very weakly developed, without nodes, and bordering the suture; 16–19 nodes are present on the sutural cord, and 21 on the peripheral keel. On last whorl, the three spiral cords fully exposed; the sutural and peripheral cords with rounded nodes; but the peripheral more developed, with stronger and a little more spaced nodes; nodes on the sutural cord upward curved, and nodes on the peripheral keel horizontally oriented; third spiral keel still lacking nodes and closer to the peripheral keel; primary axial ribs completely lacking. Fine, weak growth lines are present on the shell surface; they are opisthocline on the outer face and orthocline below the peripheral spiral keel.

Base strongly convex, with four smooth spiral cords, the innermost one nodular and stronger than others, bordering the umbilical area. The spiral cords intercept fine, weak and crowded orthocline collabral ribs.

The aperture is subcircular; the outer lip thickened, indented by external spiral cords. Columella prosocline, without tooth. A narrow pseudumbilicus is developed and clearly visible, with a diameter measuring approximately 15–22 percent of shell width.

Dimensions (mm) given in Table 2.

Etymology.—Dedicated to Juan Keidel, pioneer on the Early Jurassic geological knowledge of Chubut Province.

Types.—Holotype, MPEF-PI 1160; paratypes, MPEF-PI 1890, 1891, 1893, 1899, 1144, 1148, 1153, 1156, 4134, 4045, 4151, and 4167. 12 teleoconchs preserved as external molds.

Other material.—MPEF-PI 1140–1143, 1145–1147, 1149–1152, 1154, 1155, 1157–1159, 1161, 1162, 1164–1169, 1887–1889, 1892, 1894–1898, 3501–3507, 3539, 3540, 3552, 3553, 3556, 3557, 3559abc, 3561, 3566, 3567ab, 3570, 4025, 4048, 4055, 4057, 4065–4079, 4082, 4128–4135, 4137, 4138, 4140, 4142–4144, 4147–4154, 4157, 4158, 4159, 4160, 4162, 4163, 4166, 4169, 4170, 4171, 4182; MLP 18514, MLP 15434, MLP (1), MLP (4). 111 specimens preserved as external molds.

Occurrence.—Beds AL 35, 36, 37, 39, and 40 from Aguada Loca locality; bed BET 32 from Lomas de Betancourt locality; marine sediments at Lomas Occidentales locality; Aguada Plate locality, Early Jurassic (late Pliensbachian–early Toarcian), Mulanguñeu Formation, Chubut Province, Argentina; beds PA 06, 07, and 08 from Puesto Currumil locality; marine sediments at Cañadón Puelman locality, Early Jurassic (late Pliensbachian), Osta Arena Formation, Chubut Province, Argentina. Estación Rajapalo locality (Cordillera del Viento), Early Jurassic

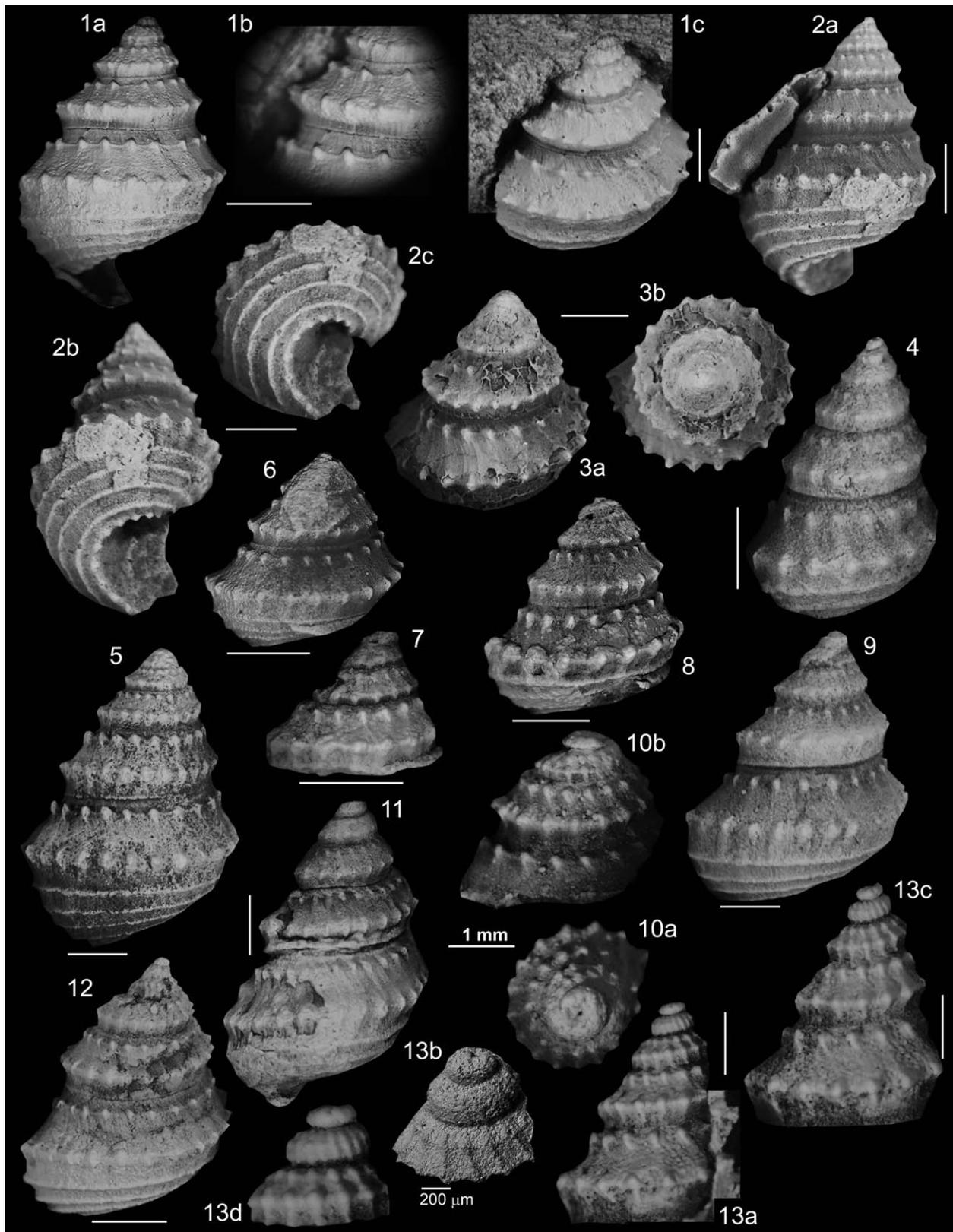


FIGURE 4—*Calliotropis (Riselloidea) keideli* n. sp. 1, MPEF-PI 1160, holotype; 1a, teleoconch in lateral view; 1b, ornament detail; 1c, apical view; 2, MPEF-PI 4167, paratype; 2a, lateral view; 2b, 2c, basal and umbilical views; 3, MPEF-PI 4130; 3a, teleoconch in lateral view; 3b, apical view; 4, MPEF-PI 1891, paratype, teleoconch in lateral view; 5, MPEF-PI 4151, paratype, teleoconch in lateral view; 6, MPEF-PI 1899, paratype, teleoconch in lateral view; 7, MPEF-PI 1168, juvenile teleoconch in lateral view; 8, MPEF-PI 1895, teleoconch in lateral view; 9, MPEF-PI 4131, teleoconch in lateral view; 10, MPEF-PI 4045, paratype, juvenile teleoconch; 10a, apical; 10b, lateral views; 11, MPEF-PI 4132, teleoconch in lateral view; 12, MPEF-PI 1148, paratype, teleoconch in lateral view; 13, MPEF-PI 4057, paratype; 13a, 13c, juvenile teleoconch in lateral view; 13b, 13d, juvenile teleoconch whorls detail. Scale bars=3 mm except where otherwise noted.

TABLE 2—Dimensions (mm) of *Calliotropis (R.) keideli* n. sp. Asterisk indicates missing data.

<i>Calliotropis (R.) keideli</i> n. sp.	Type	Height	Width	Apical angle
MPEF-PI 1142		8.6	6.4	*
MPEF-PI 1144	Paratype	10.5	8.3	*
MPEF-PI 1147		9.5	7.7	*
MPEF-PI 1148	Paratype	10	7.6	71°
MPEF-PI 1149		12.4	7.6	*
MPEF-PI 1150		10	7.1	*
MPEF-PI 1152		15.7	9.2	*
MPEF-PI 1153	Paratype	13.7	8.7	82°
MPEF-PI 1156	Paratype	13.5	8	71°
MPEF-PI 1157		13.5	7.8	*
MPEF-PI 1158		6.6	6.8	85°
MPEF-PI 1159		9.3	8.7	*
MPEF-PI 1160	Holotype	10	7.4	80°
MPEF-PI 1161		12	8.7	*
MPEF-PI 1164		10.4	9.2	*
MPEF-PI 1164		10.6	8.9	*
MPEF-PI 1165		9.5	7.5	*
MPEF-PI 1887		7.3	7.1	83°
MPEF-PI 1888		8.7	5.7	81°
MPEF-PI 1890	Paratype	11	9.2	*
MPEF-PI 1891	Paratype	10.5	5.8	75°
MPEF-PI 1893	Paratype	12.1	8.8	71°
MPEF-PI 1895		9.5	6.7	84°
MPEF-PI 1896		8.9	5	*
MPEF-PI 1898		11.9	8.5	*
MPEF-PI 1899	Paratype	7	7.2	77°
MPEF-PI 3540		8	8.1	*
MPEF-PI 3552		8.5	6.6	*
MPEF-PI 3557		16	10.8	*
MPEF-PI 3559a		9.8	9.8	*
MPEF-PI 3559c		12	8.8	*
MPEF-PI 3561		7.8	5	*
MPEF-PI 3566		11.2	9.6	*
MPEF-PI 3567a		7.3	6.6	*
MPEF-PI 3567b		8.2	7	*
MPEF-PI 3570		7	6.5	*
MPEF-PI 4134	Paratype	14	7.5	73°
MPEF-PI 4151	Paratype	13.3	9	*
MPEF-PI 4167	Paratype	11.7	7.4	75°

(Pliensbachian), Piedra Pintada Formation, Neuquén Province, Argentina.

Remarks.—Features such as a gradate to slightly coeloconical shell, first teleoconch whorl convex and smooth, mature teleoconch whorls flat to concave, with spiral and nodular elements; convex base with four spiral cords and pseudoumbilicus, and a subcircular aperture separate *Calliotropis (Riselloidea) keideli* n. sp. from other similar members of the genus. *C. (R.) keideli* is the first confirmed record of the genus (and subgenus) in the Jurassic of Argentina and South America.

The shell characters of *C. (R.) keideli* fit very well the diagnosis of Calliotropini of Hickman and McLean (1990) being strikingly similar to the extant members of the group. *Calliotropis (Calliotropis) ottoii* (Philippi, 1844), the type species of *Calliotropis*, lives in the northwestern and northeastern Atlantic Ocean, south Mediterranean Sea and Indonesia, in a water depth of 85–1000 m. *Calliotropis (R.) keideli* resembles *C. (C.) ottoii*; they share a similar general shell morphology and ornament pattern; the type species, however, differs from *C. (R.) keideli* in having a first teleoconch whorl with 22 orthoconical to slightly prosocline axial ribs, a broader shell shape and a more depressed spire with a ratio H/W of 0.66, the third spiral keel stronger with nodes more developed and conspicuous, base with 4–6 spiral and nodular keels, and a rather narrow umbilicus with one granular spiral cord inside (Kaim 2004, p. 23, fig. 9A).

The shells of many extant species of *Calliotropis* are very similar to the Jurassic representative here described. One of them is *Calliotropis (Calliotropis) conooides* Vilvens (2007) from Solomon Islands; however, the living species differs from the Jurassic one in having a first teleoconch whorl with 20 slightly

prosocline axial ribs, larger shell, a teleoconch consisting of nine conical whorls, the third spiral keel much stronger and the adapical keel with more conspicuous nodes, and in having a subelliptical aperture. *Calliotropis (Calliotropis) excelsior* Vilvens, 2004 from Fiji Islands and New Caledonia, differs from the Argentinean species in having a larger shell, a teleoconch comprising eight whorls, primary keels with more elongated and prosocline nodes present in number of 80–90 per whorl approximately, a strongly developed sutural ramp, and a rather wide umbilicus with a diameter of 25–28 percent of shell width. *Calliotropis (Calliotropis) acherontis* Marshall (1979, p. 529, figs. 3L–3O, 9A, 9B) from the southwestern Pacific and southwestern Indian Ocean, represents another extant member similar to *C. (R.) keideli*; however, Marshall's species is smaller than *C. (R.) keideli*, the first whorl has only 14 weakly prosocline axial ribs which develop on all teleoconch whorls, nodes are more conspicuous at the intersection points of axial and spiral elements, and are present in number of 15 per whorl on the primary spiral keels, and has a narrow umbilicus. *Calliotropis (Calliotropis) infundibulum* (Watson, 1879) (in Marshall, 1979, p. 531, figs. 4E–4G, 9C–F; Vilvens, 2004, p. 29, figs. 27, 28; Vilvens, 2007, p. 11, figs. 84, 85; Vilvens and Swinnen, 2008, p. 24, figs. 1–8, 13–20), widely distributed in the western and eastern Atlantic Ocean, Indo Pacific Ocean and South Africa, differs from *C. (C.) keideli* in being larger, slightly cyrtocircular, larger with a teleoconch consisting on 7.5 whorls, the third spiral keel more developed and nodular, a wide umbilicus without spiral keel inside and, in some specimens, the adapical keel may divide into two cords giving three cords instead of two. Finally, *Calliotropis (Calliotropis) helix* Vilvens (2007, p. 8, figs. 12–15), from Taiwan and South China Sea, is slightly more elongated than the Argentinean species, the teleoconch consists of eight whorls, the first teleoconch whorl has 20 slightly oposthocline axial ribs, the abapical spiral keel is absent on mature whorls, and the aperture is subelliptical and the umbilicus is moderately wide with crowded axial ribs inside.

Calliotropis, Calliotropis (Riselloidea) biarmata (Münster, 1844) from the Middle and Upper Jurassic of Europe (Gründel, 2000, p. 229, pl. 7, figs. 1–3; Conti and Monari, 2001, p. 200, figs. 6, 21–26; Kaim, 2004; p. 22, fig. 9 B–9E) is also very similar to *C. (C.) keideli*. However, the European species is much smaller than *C. (R.) keideli*, the first teleoconch whorl has 36–37 prosocline primary axial ribs, nodes on spiral keel are stronger, the third spiral keel is more developed with strong and more conspicuous nodes, the axial ribs on teleoconch are more developed during ontogeny, the base is slightly convex with nodular spiral keels, and it has neither umbilicus nor pseudoumbilicus.

Calliotropis (Riselloidea) vierowiensis (Gründel, 2000) (p. 229, pl. 6, figs. 16, 17; Gründel, 2003c, p. 153, pl. 5, figs. 6, 7) from the Middle Jurassic (Callovian) of Germany, resembles *C. (C.) keideli*; Gründel's species, however, has fewer teleoconch whorls (4.5), two secondary spiral keels are present on the outer face, nodes are more rounded, the base is slightly convex and ornamented by more than 15 spiral furrows, and a pseudoumbilicus is absent. *Calliotropis (Riselloidea) naybandensis* (Nützel and Senowbari-Daryan, 1999) (p. 100, pl. 1, figs. 7–9, pl. 7, figs. 4, 5) from the Upper Triassic (Norian–Rhaetian) of Central Iran, is similar in size and general shell morphology to the Argentinean form; however, the Iranian species has three primary spiral keels on the outer face of the whorls, and between them, several secondary spiral keels are present. *C. (R.) naybandensis* has also 19 axial ribs developed on all teleoconch whorls, the base is ornamented by three nodular spiral threads, and it has no pseudoumbilicus.

Calliotropis (Riselloidea) aliabadensis (Nützel and Senowbari-Daryan, 1999) (p. 101, pl. 1, figs. 10, 11, pl. 7, figs. 1–3), which is a type species of *Trochonodus* Nützel, et al., 2003 from the Upper Triassic of Iran, differs from *C. (R.) keideli* by its three strong primary spiral keels on each teleoconch whorl, the third keel being the strongest, the base has four spiral keels with rounded nodes, and the aperture is subquadrangular. We consider *Trochonodus* to be a junior synonym of *Riselloidea* though it might be also another subgenus of *Calliotropis*. *Calliotropis (Riselloidea) multistriata* (Böckh, 1874), from the Early Jurassic (Sinemurian–Pliensbachian) of Hungary (Szabó, 1982, p. 25, pl. 3, figs. 3–6; 2009, p. 82, fig. 77), is also comparable to *C. (C.) keideli*; but the Hungarian species has the outer face of whorls more convex than the Argentinean species. Four primary spiral keels are developed on all teleoconch whorls, regularly spaced prosocline growth lines are present on the shell surface, and nodes at intersection points of spiral and collabral elements are weaker than in the Argentinean species. *Calliotropis (Riselloidea) noszkyi* (Szabó, 1995) (p. 71, pl. 7, fig. 13; 2009, p. 83, fig. 78) from the Early Jurassic (Sinemurian) of Hungary, differs from *C. (R.) keideli* in having three primary spiral keels visible on last teleoconch whorls, collabral and regularly spaced growth lines on the shell surface, and strongly convex teleoconch whorls. *C. (R.) keideli* is similar to *Calliotropis (Riselloidea) vaihingensis* (Brösamlen, 1909) from the Early Jurassic (upper Hettangian) of Germany (Gründel, 2003a, p. 17, pl. 5, figs. 2–5); the former species, however, is slightly more conical than *C. (R.) keideli*, has more developed axial ribs on all growth stages. *Calliotropis (Riselloidea) pileiformis* (Jaitly et al., 2000) (p. 56, pl. 5, figs. 15, 16, pl. 6, figs. 1–3), from the Middle Jurassic (Bathonian) of India, resembles also *C. (R.) keideli*; however, in *C. (R.) pileiformis* 20 axial ribs appear later, which increase in strength toward the mature whorls; the adapical keel is divided into two spiral keels from the third teleoconch whorl, the third keel is peripheral on all teleoconch whorls, and the base is flatter with four strongly nodular spiral keels. *Trochonodus iranicus* Nützel et al., 2003 (p. 2, pl. 24, figs. 1–4), from the Upper Triassic (Norian) of Iran, shares some features with *C. (C.) keideli*; the Iranian species, however, has more convex whorls, has 16 slightly prosocline axial ribs per whorl, the primary spiral ribs are weaker than the axial ribs, and it lacks an umbilicus. *Calliotropis (Riselloidea) erraticus* Gründel and Koppka, 2007 (p. 648, pl. 1, figs. 1–5), from the Early Jurassic of Germany, resembles *C. (R.) keideli*; however, the European species is slightly smaller than the Argentinean form, with a rather depressed spire, first teleoconch whorl have 19 separate and thick axial ribs, the abapical keel appears on the third whorl, and the adapical keel on the fourth whorl; nodes are acute, spaced and equally developed on both spiral keels, and the base has a small and narrow umbilicus. *C. (R.) keideli* resembles also *Calliotropis (Riselloidea) lorioli* (Greppin, 1898), from the Middle Jurassic (Bajocian) of Germany; the latter species, however, has three primary and nodular spiral keels on the outer face of the whorls, nodes are more rounded than in the Argentinean species, the base has 2–3 spiral keels, the inner lip forms a broad columellar callus, and it has no umbilicus (Gründel, 2003b, p. 65, pl. 6, figs. 9, 10). *Calliotropis (Riselloidea) toralolensis* Kiel and Bandel, 2001 and *Calliotropis (Riselloidea) seguris* Kiel and Bandel, 2001 (p. 140, pl. 1, figs. 4, 5, 7) from the Upper Cretaceous (Campanian) of Spain, differ from *C. (R.) keideli* in having a more straight shell outline, four spiral rows of small and less developed nodes, and a narrow umbilicus; and in having a more developed spiral keel, small and rounded nodes on the outer face of the shell, and the umbilical area with many tuberculate spiral lines, respectively. Finally, *Calliotropis (Calliotropis) antarchais* Stilwell (2005, p. 11, fig. 2A–2J) from the Eocene of Antarctica resembles the *Calliotropis* species here described; however, the Antarctic species

has a more reticulate ornament pattern on early teleoconch whorls, the teleoconch whorls rapidly expanding, a less developed sutural ramp, an elliptical aperture and a flatter base.

CALLIOTROPIS (RISELLOIDEA) cf. *C. (R.) KEIDELI*
Figure 5.9

2011 *Calliotropis keideli* Ferrari, p. 56, pl. 4, figs. 1, 2.

Description.—Dextral, trochiform, pagodiform, slightly coelocoidal and high-spined shell. Shell rather small for the genus. Apertural, basal and umbilical characters unknown.

Protoconch is not preserved. Teleoconch of five whorls, in the juvenile whorls the outer face is slightly concave becoming flat and vertical abapically; last teleoconch whorl becomes moderately convex or cyrtocoidal. The teleoconch bears five spiral nodular cords and axial ribs on the shell surface; nodes produced by the intersection of cords with axial elements. Suture impressed.

First teleoconch whorl convex, seemingly lacking axial ribs. On second teleoconch whorl, two primary spiral cords visible; the peripheral slightly stronger than the sutural cord, both with nodes at intersection points with axial ribs; nodes are small and rounded, and stronger on the peripheral keel; primary axial ribs prosocline and opisthocyrt on the surface of whorls, and orthocline abapically; on the lower portion of the whorls, axial ribs become orthocline. On third whorl, a third abapical spiral cord emerging very weakly from suture; the peripheral keel still stronger than the sutural cord; nodes rounded to acute. On fourth whorls, the third cord visible, very weakly developed, without nodes, and bordering the suture on the outer face of the whorl; nodes are present in number of 20–25. On last whorl, the peripheral keel and sutural cord completely visible, both with small, separate and acute nodes, but a little more developed on the peripheral one; two fine, small and crowded secondary spiral cords appear on the outline of the whorl between the primary keels; axial ribs still visible and slightly prosocline, connecting nodes of primary and secondary spiral cords; the third cord is covered on last whorl. Basal, apertural and umbilical characters are not preserved.

Dimensions (mm): MPEF-PI 1163; height, 13.4 mm; width, 8.35 mm; apical angle, 70°.

Material.—MPEF-PI 1163; specimen preserved as external mold.

Occurrence.—Bed AL 39 at Aguada Loca locality, Early Jurassic (late Pliensbachian–early Toarcian), Mulanguñeu Formation, Chubut Province, Argentina.

Remarks.—The species here described is very similar to *C. (R.) keideli*, however, it has orthocline to slightly prosocline axial ribs on all teleoconch whorls; the first teleoconch whorl apparently lacks the characteristic axial ribs of *C. (R.) keideli*; an almost median angulation at the abapical spiral cord; and last teleoconch whorl is convex or cyrtocoidal with two crowded secondary spiral ribs. Open nomenclature is used here for this species until more material is available.

CALLIOTROPIS (RISELLOIDEA) sp.
Figure 5.10

2011 *Calliotropis* sp. Ferrari, p. 69, pl. 5, figs. 7–11.

Description.—Dextral, pagodiform to slightly coelocoidal and moderately high-spined shell. Shell of rather small size for the genus; ratio H/W 0.94.

Protoconch is not preserved. Teleoconch fragmentary, up to four preserved whorls, the surface of the whorls is flat to slightly concave. The teleoconch bears two visible spiral and nodular cords, axial ribs, and collabral elements on the shell surface. On the last two whorls nodes are produced by the intersections of the cords with primary axial elements. Suture impressed.

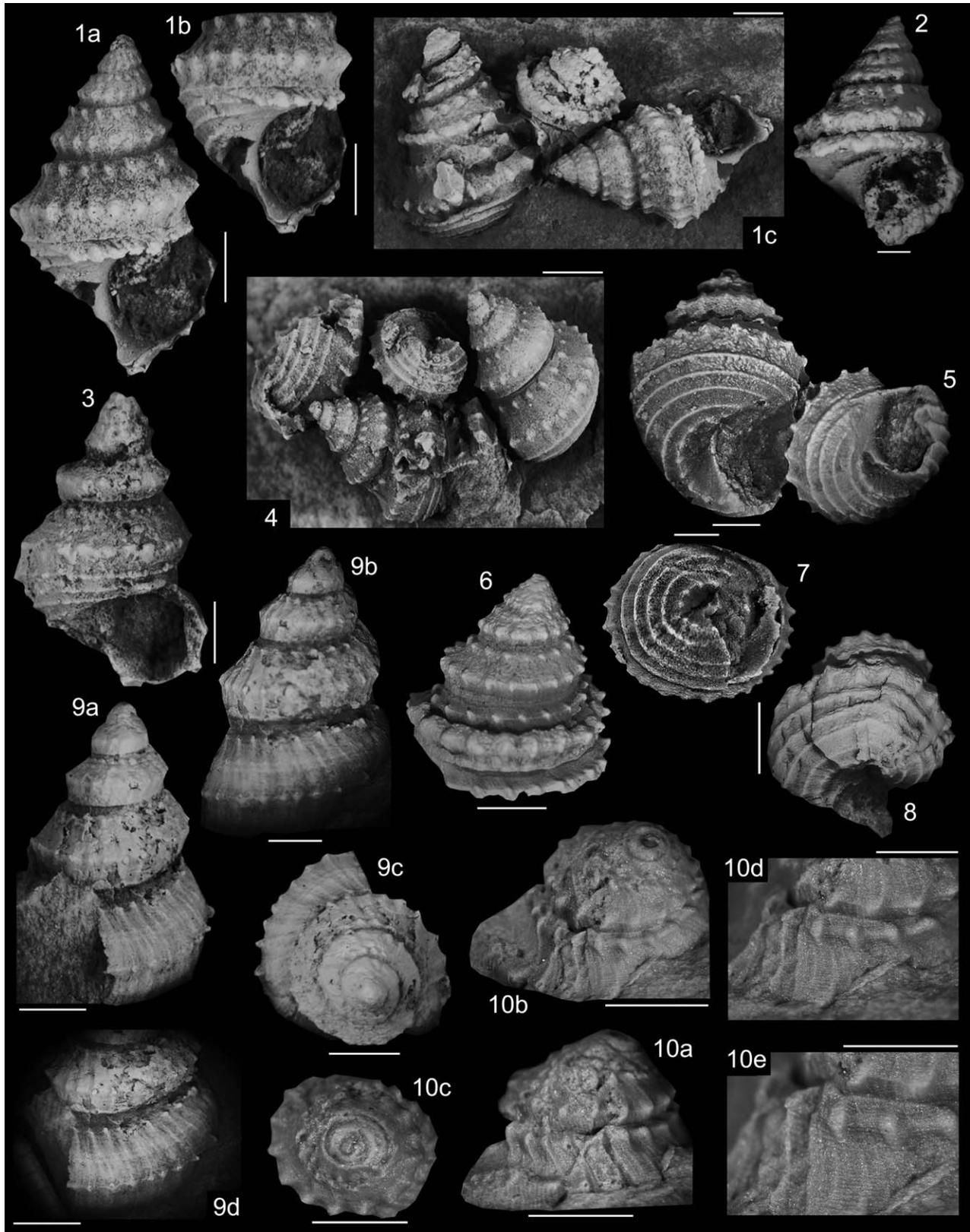


FIGURE 5—1–8, *Calliotropis (Riselloidea) keideli* n. sp. 1, MPEF-PI 4134, paratype; 1a, teleoconch in lateral and apertural views; 1b, apertural, basal and umbilical detail; 1c, three associated specimens in lateral, basal and apertural views; 2, MPEF-PI 4068, lateral and apertural views; 3, MPEF-PI 1156, paratype, teleoconch in lateral and apertural views; 4, MPEF-PI 4131, four associated specimens in lateral and basal views; 5, MPEF-PI 1153, paratype; 5, two associated specimens in basal, umbilical and apertural views; 6, MPEF-PI 1158, teleoconch in lateral view; 7, MPEF-PI 1144, paratype, basal and umbilical views; 8, MPEF-PI 1890, paratype, basal and umbilical views; 9, *Calliotropis (Riselloidea)* cf. *C. (R.) keideli*, MPEF-PI 1163; 9a, 9b, teleoconch in lateral view; 9c, teleoconch in apical view; 9d, last whorl ornament detail; 10, *Calliotropis (Riselloidea)* sp. MPEF-PI 3554; 10a, 10b, teleoconch in lateral view; 10c, teleoconch in apical view; 10d, 10e, ornament detail. Scale bar=3 mm.

First teleoconch whorl convex and smooth. At the end of first whorl or at the beginning of second whorl, a peripheral keel appears weakly. On second teleoconch whorl, the peripheral keel is slightly more developed than the sutural cord, with rounded nodes. On third whorl, both primary spiral keels completely visible, and the peripheral keel still stronger than sutural cord, with acute and stronger nodes; primary axial ribs connecting nodes of spiral threads; a reticulated ornament of secondary and regularly spaced spiral cords and opisthocyrt growth lines are present on the ramp of the whorl; the growth lines become orthocone toward the outer face of the whorl. On last whorl, the peripheral keel stronger and developed, with acute and separate nodes; the axial ribs and the reticulated ornament pattern of secondary spiral cords and growth lines are still present. Basal, umbilical and apertural features unknown.

Material.—MPEF-PI 3554; one fragmentary specimen preserved as external mold. Dimensions (mm): MPEF-PI 3554. Height, 6.6 mm; width, 7 mm.

Occurrence.—Bed BET 33 from Lomas de Betancourt fossiliferous locality, Early Jurassic (late Pliensbachian–early Toarcian), Mulanguineu Formation, Chubut Province, Argentina.

Remarks.—The single specimen described shows the diagnostic characters of *Calliotropis*. However, some important features, such as the aperture, base and umbilical area are not preserved, so, it is left in open nomenclature until new material is available.

Calliotropis (*R.*) sp. differs from *C. (R.) keideli*, in having a reticulate ornament formed by secondary and regularly spaced spiral cords and opisthocyrt growth lines; lack of axial ribs on first teleoconch whorl, and of a nodular spiral keel in the sutural area.

SUMMARY

Vetigastropoda is one of the largest and most archaic groups of gastropods with numerous lineages apparently rooted back in the late Cambrian (Knight et al., 1960). Phylogenetic relationships among vetigastropod subgroups are increasingly better understood using both morphological and molecular data, nevertheless not yet fully assessed (Kano, 2008).

The most diverse clade among vetigastropods is the superfamily Trochoidea (Hickman, 1996). Trochoideans (*sensu* Hickman and McLean, 1990) are known worldwide from the tropics to the polar regions, and from the shallowest intertidal zone to bathyal depths. They are also morphologically diverse and live in a variety of habitats. Hickman and McLean (1990) suggested that they have an extensive fossil record ranging back to the Middle Triassic, though gastropods similar to trochoideans are reported from as early as the Ordovician (Hynda, 1986; Dzik, 1994a, 1994b). It seems, however, that trochoideans as they were understood in the twentieth century are a polyphyletic group. The molecular analyses of Kano (2008) and Kano et al. (2009) showed, for instance, that the deep-sea Superfamily Seguenzioidea, a monophyletic group of Vetigastropoda, consists of not only of the family Seguenziidae, but also the trochoid-like families Calliotropidae, Chilodontidae and Cataegidae. This result supports earlier reports by McLean (1982) who observed that some living “trochids” (e.g., *Calliotropis*, *Turcica*, *Bathybembix*, *Cidarina*, *Danilia*, and *Euchelus*) are characterized by character states that are more primitive than those of the remaining members of the group. All these genera are now considered to be seguenzioideans. It has therefore not been surprising that this group has been richly represented in the fossil record and many taxa which preliminarily were identified as trochoideans turned out to be seguenzioideans. Fossil members of this group were united in the family Eucyclidae (e.g., Kiel and Bandel, 2001; Kaim, 2004)

strongly reminiscent of the Recent Calliotropidae (Kaim, 2004). It seems to be clear now that the families Eucyclidae Koken, 1897 and Calliotropidae Hickmann and McLean, 1990 are synonymous, with Eucyclidae having priority (e.g., Kaim, 2004).

Recent eucyclids (=calliotropids) are abundant, diverse and widely distributed gastropods. They are particularly common in the Indopacific Ocean, Atlantic coast of Europe, Africa, Madagascar, Brazil, and Chile reaching up to Antarctica. This distribution shows a wide range of climatic conditions to which these mollusks have adapted. This adaptational ability is also well visible in the wide range of their bathymetric occurrences, though they are most common in a depth range from few hundreds meters to more than 3,200 m (Vilvens, 2007). Extant eucyclids are still classified based on a set of shell characters (mineral composition and microstructure; number of spiral ribs and nodes on its surface, base and umbilical area; spire height; and absence or presence of umbilicus; see Vilvens and Swinnen, 2008), though anatomical and genetic information on this group is now improving (McLean, 1982; Kano, 2008; Kano et al., 2009).

As outlined above, ancient eucyclids are ubiquitous in the fossil record and well known from the Mesozoic of Europe and Asia. The present paper adds first certain records of the group from the Jurassic of South America, and the detailed shell information of the Argentinean eucyclid taxa may greatly assist in lineage studies of this morphologically complex group. In contrast to living species of *Calliotropis*, Mesozoic forms were also common in shallow marine environments. Apparently, in the latest Mesozoic or earliest Cenozoic, eucyclids started to demise from the shallow water environments, with majority of taxa inhabiting bathyal depths.

The new record of *Calliotropis* in the early marine Jurassic (late Pliensbachian–early Toarcian) of South America extends the range of the Mesozoic eucyclid occurrences to the Gondwanan seas.

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