A new caenogastropod from the upper Rhaetian of Lombardy: Palaeobiogeographical history and implications for the Early Jurassic gastropod recovery

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Pieroni, V., Monari, S., and Todd, J.A. 2021. A new caenogastropod from the upper Rhaetian of Lombardy: Palaeobiogeographical history and implications for the Early Jurassic gastropod recovery. *Acta Palaeontologica Polonica* 66 (1): 193–206.

A new gastropod genus and its type species, namely *Ederazyga fanchini* gen. et sp. nov., are described from the upper Rhaetian deposits of Lombardy (northern Italy) and tentatively placed into the family Zygopleuridae. The first appearance of *Ederazyga* is recorded in the lower Carnian deposits of Southern Alps and the stratigraphical distribution of the genus ends almost at the Triassic/Jurassic boundary. Its occurrence in Norian beds of the Nayband Basin (central Iran) suggests an eastward extension of the distribution during that time. *Ederazyga* is probably one of the Alpine gastropod taxa appearing in this area after the formation of the basin. The genus is possibly related to a group of Early Jurassic, medium to large *Zygopleura*-like species that are well represented in the Sinemurian and Pliensbachian carbonate platform deposits of the Mediterranean region and in the Hettangian to Pliensbachian successions of the European epicontinental shelf. This group shows an apparent species radiation in these areas testifying to the gastropod recovery following the Late Triassic decline in biodiversity. *Ederazyga fanchini* is shown to be congeneric with *Cerithium*? *lateplicatum* Klipstein, 1843, which is the type species of *Camponaxis* Bandel, 1995. The definition and diagnosis of *Camponaxis* was based on specimens that are clearly different, at generic and higher taxonomic levels, from the holotype of *C.*? *lateplicatum*. They belong to a distinct species here named *Camponaxis bandeli* sp. nov. Several species have been subsequently ascribed to *Camponaxis* following its original diagnosis. Therefore, we invoke ICZN Art. 70.3.2 in order to preserve the unambiguous identity of the genus and to ensure its nomenclatural stability. *Camponaxis bandeli* is fixed as the new type species for *Camponaxis* and *C.*? *lateplicatum* is here assigned to *Ederazyga*.

Key words: Gastropoda, Zygopleuridae, systematics, palaeobiogeography, faunal recovery, Jurassic, Late Triassic, Italy, Southern Alps.

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Received 7 July 2020, accepted 26 August 2020, available online 4 January 2021.

Introduction

The Late Triassic gastropod record is characterized by a strong and progressive post-Carnian decrease in species richness that reaches its nadir in the Rhaetian (Nützel 2005). This trend most probably reflects a real decrease in overall diversity but detailed studies on the changes in taxonomic diversity and their timing as well as the possible taphonomic control of the record are currently lacking. The interpretation of the Rhaetian record is particularly problematic since the available data are of a quite low overall quality. Apart from the studies on the relatively diverse faunas of the Nayband Basin (central Iran) described by Nützel and Senowbari-Daryan (1999) and Nützel et al. (2003, 2010) and other more sparse contributions (e.g., Bandel 1994; Barker and Munt 1999; Begg and Grant-Mackie 2003; Hasibuan and Grant-Mackie 2007; Ferrari 2015), literature on Rhaetian gastropods is significantly outdated. This is especially the case for the Alpine region. Sources reporting systematic studies, though relatively numerous, date back to the nineteenth century and the more recent ones are at least fifty years old

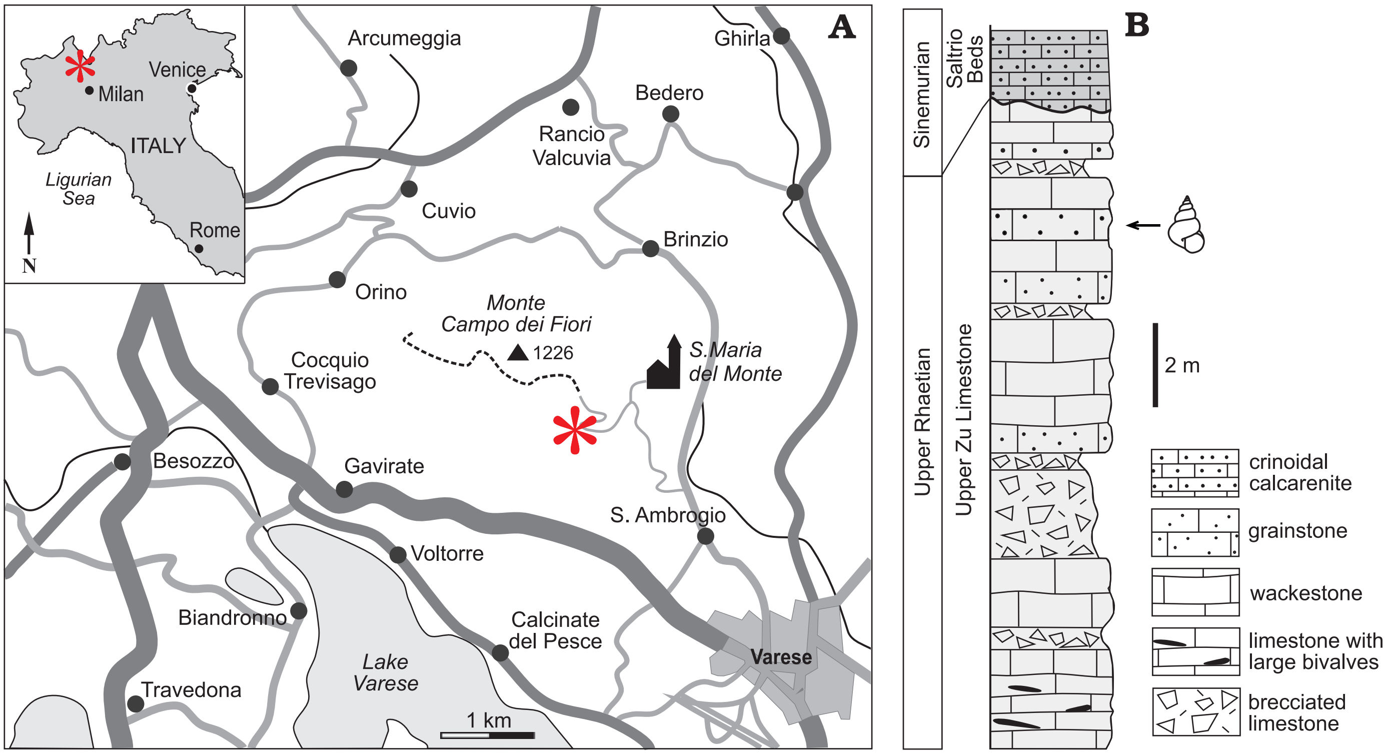

Fig. 1. Location of the outcrop (**A**) and stratigraphical section (**B**) modified from Jadoul et al. (2005).

(Escher von der Linth 1853; Winkler 1859, 1861; Stoppani 1857, 1860–1865; Dittmar 1864; Fischer-Ooster 1870; Ammon 1878, 1893; Lepsius 1878; Schäfer 1888; Haas 1909; Kittl and Spengler 1916; Desio 1929; Osswald 1930; Parona 1932; Borghi 1938; Kühn 1942; Chiesa 1949; Zapfe 1949, 1962, 1963, 1965, 1967; Conti 1954). Most of these papers concern gastropod faunas from the thick carbonate platform units of the Northern Calcareous Alps and Southern Alps where the fossils are frequently poorly preserved, difficult to isolate from the hard matrix or preserved as moulds. Their state of preservation obviously limits systematic analysis and the interpretation of the data. On the other hand, the study of these faunas is crucial to understand the reasons for the impoverishment of the Late Triassic gastropod record and the dynamics of the Early Jurassic recovery that helped shape the subsequent evolutionary history of this group.

In this paper a new gastropod genus and its type species are erected on the basis of specimens preserved as moulds obtained from the upper Rhaetian carbonate platform beds of Lombardy (northern Italy). Through taking into account the state of preservation and the poor information on the coeval faunas, a tentative reconstruction of the biogeographical history of the genus is proposed and its possible relationships with Early Jurassic gastropods are investigated. Since the facies, lithology and quality of preservation of most of the Rhaetian Alpine gastropod faunas listed above are comparable to those of the material described here, both the constraints and potential shown by this study are suggestive of what one can expect from a future revision of these faunas.

Institutional abbreviations.—GPIH, Geologisch-Paläontologisches Institut, Universität Hamburg, Hamburg, Germany; MRZ, Museo delle Regole "Rinaldo Zardini", Cortina d'Ampezzo, Belluno, Italy; MSNVI, Museo Scientifico Naturalistico "A. Stoppani", Venegono Inferiore, Varese, Italy; NHMUK, The Natural History Museum, London, United Kingdom; RGM, Rijksmuseum van Geologie en Mineralogie, now Naturalis Biodiversity Centre, Leiden, The Netherlands.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:30E06C37-5516-476A-B14D-C7CB44A8DFEB.

Geological setting

The material comes from Le Ville (Villa de Grandi and Villa Edera) (DMS 45°51'48"N 8°46'29"E), a locality at about 900 m altitude on the southern side of Monte Tre Croci, a peak of the Monte Campo dei Fiori mountain group (Varese, Lombardy, northern Italy) (Fig. 1A). The Upper Triassic–Lower Jurassic stratigraphy and the palaeogeographic evolution of Lombardy have been the subject of many recent studies (e.g., Jadoul et al. 1994, 2004, 2005; Galli et al. 2005, 2007; Jadoul and Galli 2008; Tackett and Bottjer 2012). The Monte Campo dei Fiori area and Villa Edera section, were specifically treated by Jadoul et al. (2005) to which we refer readers for further information. In the area of Monte Campo dei Fiori, the Rhaetian deposits are represented by platform carbonates of the Zu Limestone Formation. The succession is reduced in thickness and represents the deposition on a structural high bordering the eastern side of the Monte Nudo Basin (western Lombardy). In the Villa Edera section only the upper part of the unit crops out (upper Zu Limestone, upper Rhaetian; Fig. 1B) and consists of grainstone, wackestone and brecciated carbonates representing a cyclic transition from beach to tidal and subaerial environments. The top of the upper Zu Limestone is cut by an unconformity which is easily recognizable across the whole of western Lombardy. This surface is often associated with brecciated limestone and reflects a subaerial exposure event in the Hettangian. The material described here comes from a light nutbrown biocalcarenite bed about three metres below this surface where it is associated with *Conchodon infraliasicus* Stoppani, 1865, and other bivalves. In the Villa Edera section the Hettangian unconformity is capped by the Saltrio beds, a Sinemurian unit consisting of grey and crinoidal calcarenite deposited in subtidal conditions.

Molluscs from the Rhaetian succession of Monte Campo dei Fiori are mainly represented by bivalves. The locality was indicated by Stoppani (1857, 1860–1865) as yielding part of the material from which the author erected *C. infraliasicus* (see Teruzzi 2015 for details). Kutassy (1933) also described some bivalves from outcrops in this area. In contrast, no gastropods were mentioned by Stoppani (1860–1865) from Monte Campo dei Fiori, although the author described numerous Rhaetian species from Lombardy. Chiesa (1949), however, listed about ten species that seemingly come from the same stratigraphical interval yielding the material studied here. In addition, indeterminable molluscs have been frequently recorded in thin section from Rhaetian deposits of this and neighbouring areas (e.g., Wiedenmayer 1963; Jadoul et al. 2005).

Material and methods

The material of the new species *Ederazyga fanchini* consists of two specimens deposited at the Museo Scientifico Naturalistico “A. Stoppani”, Venegono Inferiore (Varese, Lombardy, Italy) (MSNVI). One of them is represented by an external mould and its internal mould. The systematic study was made possible by the good preservation of the external mould. Its rubber cast represents slightly more than the axial half of the shell and reproduces with good detail both the apical spire and the adult shell. A full definition of the new genus described here required a review of the taxonomic status of *Cerithium*? *lateplicatum* Klipstein, 1843, type species of the genus *Camponaxis* Bandel, 1995, whose type material, stored at the Natural History Museum, London (UK), has been restudied. The systematic arrangement at higher taxonomic rank follows Bouchet et al. (2017). The photographs of *E. fanchini* have been made with the focus stacking method on the specimens coated with ammonium chloride and elaborated with Helicon Focus Pro 6.7.1 software.

Systematic palaeontology

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox, 1960

?Superfamily Pseudozygopleuroidea Knight, 1930

?Family Zygopleuridae Wenz, 1938

Remarks.—The uncertain suprageneric attribution of *Ederazyga* gen. nov. is due to the lack of information on the protoconch. The genus is tentatively placed into the family Zygopleuridae Wenz, 1938, superfamily Pseudozygopleuroidea Knight, 1930, on the basis of the characters of the adult shell and the similarities with other zygopleurid taxa (see below for comparisons). Characters suggesting zygopleurid affinities are the slender shell with strongly convex, pendent whorls and the dominant axial ornament of prominent, opisthocline and sinuous collabral ribs made by distinctly parasigmoidal growth lines.

Genus *Ederazyga* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:6E6B074A-0672-41C1-8D53-7177DEA7A187

Etymology: After Villa Edera, type locality of the type species, and the suffix *-zyga*, referring to the probable zygopleuroidean affinities of the taxon.

Type species: *Ederazyga fanchini* sp. nov.; see below.

Species included: The following additional species, listed in stratigraphical order, are here ascribed to *Ederazyga*: *Cerithium*? *lateplicatum* Klipstein, 1843 (see below for references), lower Carnian, eastern Dolomites (Southern Alps, northern Italy); *Striazyga*? sp. in Kaim et al. (2006: 477, fig. 4E, F, H), Carnian, Karavanke Mountains (Slovenia); *Katosira*? *lateplicata* (Klipstein, 1843) sensu Nützel et al. (2012: 56, fig. 3G), upper part of middle Norian, Natanz region (central Iran).

Diagnosis.—Shell medium to large sized, fusiform to high-pagodiform. Adult whorls strongly convex, variably pendent in outline, with inflated peripheral region placed at or slightly below middle of whorl surface. Adapical part of whorl surface gently concave. Base subconoidal. Peristome with anterior opening ranging in shape from a short spout to a distinct canal. Collabral ornament composed of prominent opisthocline ribs, slightly to markedly swollen on peripheral band. Spiral ornament composed of sharp threads overlapping collabral ribs and producing a rough shell surface. Base with same ornament pattern as that of spire whorls.

Remarks.—The species belonging to *Ederazyga* gen. nov. have shells of medium to large adult size, attaining a height of a few centimetres to slightly more than ten centimetres. In addition to the diagnostic characters listed above, the last whorl tends to be more expanded, subventricose, with respect to the spire whorls, and the sharpness of the spiral ornament makes the surface of the shell slightly rough. In the type species, namely *Ederazyga fanchini* sp. nov., the peristome is reflected outward at the junction of the basal lip with the columellar lip and forms a short, shallow and wide lower spout. The apical spire is poorly preserved. The

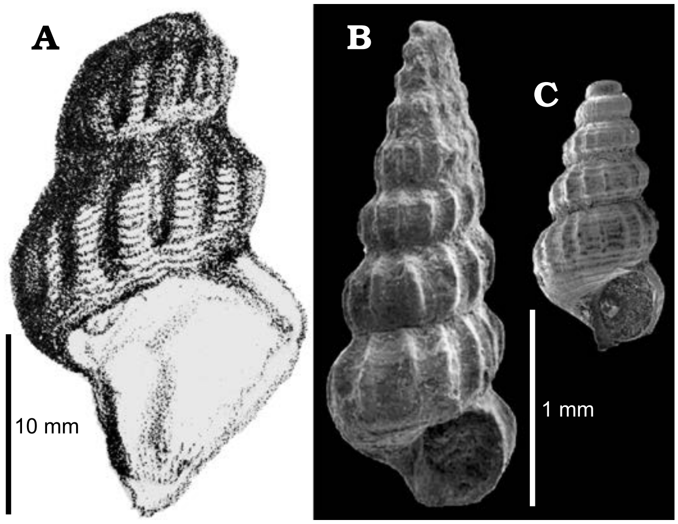

Fig. 2. Comparison between the holotype of zygopleurid? gastropod *Cerithium*? *lateplicatum* Klipstein, 1843 and the specimens illustrated by Bandel (1995), here ascribed to a tofanellid *Camponaxis bandeli* sp. nov.; lower Carnian, eastern Dolomites (Southern Alps, northern Italy). **A**. Fragmentary type specimen (NHMUK PI OR 35701) of *Cerithium*? *lateplicatum*, original illustration from Klipstein (1843: pl. 11: 35). **B**, **C**. *Camponaxis bandeli* sp. nov. **B**. Holotype, adult shell (RGM 219 039), from Bandel (1995: pl. 14: 5). **C**. Paratype, juvenile shell (RGM 219 040), from Bandel (1995: pl. 14: 3). Reproduced accordingly to CC-BY 4.0 license.

collabral and spiral ornament are visible from the second preserved whorl and it is not clear if the previous whorl is smooth or provided with a weak collabral ornament. The other described species here assigned to *Ederazyga* differs from the type species in having a more slender, turriculate-fusiform shell whereas in *E. fanchini* the shell is subpagodiform. This is the only observable difference and is not sufficient to justify their separation at genus rank.

Cerithium? *lateplicatum* Klipstein, 1843, shows several distinctive characters of *Ederazyga*: the size of the shell, the shape of the whorls and the ornament pattern. This species, here re-described (see below), was selected by Bandel (1995) as type species of the genus *Camponaxis* Bandel, 1995 (family Tofanellidae Bandel, 1995, superfamily Mathildoidea Dall, 1889). However, the definition of this genus, including its formal diagnosis, was based on specimens (Bandel 1995: 27, pl. 13: 9, pl. 14: 1–5) erroneously ascribed by this author to Klipstein's (1843) species, as also pointed out by Nützel et al. (2012). The differences are obvious especially when one considers the size of the shell (Fig. 2). The type material of *C*.? *lateplicatum* is represented by a single fragmentary specimen (NHMUK PI OR 35701) that corresponds to the shell illustrated by Klipstein (1843: 182, pl. 11: 35) (Fig. 2A). Consequently, it is the holotype of the species by monotypy. The specimen, which preserves only the last two whorls, is 28 mm high and the reconstructed height of the shell is about 40 mm. In contrast, the height of the bigger shell illustrated by Bandel (1995) is 2.5 mm (Fig. 2B) and the author reported 4.5 mm as the maximum height observed in his material. According to Bandel (1995), his specimens represent immature shells of Klipstein's (1843) species. However, some characters described by him, such as the high number of whorls (slightly less than ten), and the full development of the ornament, would indicate that at least the larger specimens represent subadult or adult shells. In addition, the peristome shows a slight anterior spout or sinus whereas in the holotype of *C*.? *lateplicatum* the peristome has a distinct anterior canal. Bandel's (1995) shells belong to a distinct species here named as *Camponaxis bandeli* sp. nov., pro *Camponaxis lateplicata* (Klipstein, 1843) in Bandel (1995), non Klipstein (1843). The holotype, here selected, is the shell RGM 219 039 figured by Bandel (1995: pl. 14: 5) and refigured as Fig. 2B herein. Two additional specimens illustrated by Bandel (1995) are selected here as paratypes: one specimen is figured by this author on pl. 13: 9 and pl. 14: 1, 2, 4; the other specimen is figured on pl. 14: 3. As stated by Bandel (1995), the holotype is stored at RGM and comes from the lower Carnian (*Trachyceras aonoides* Zone) St. Cassian Formation of Dibona, eastern Dolomites (northern Italy) and the paratypes are from the same stratigraphical level but from the locality of Misurina in the same region. The paratypes are apparently registered as RGM 219 040 in Bandel (1995: 27), though noted on the explanation to plate 14 as being housed in the GPIH. The species has been adequately described by Bandel (1995: 27) and its species epithet we dedicate to this author. Several species have been ascribed to the genus *Camponaxis* (e.g., Bandel 1995; Bandel et al. 2000; Gründel and Nützel 2013, 2015; Nützel and Gründel 2015). They are quite comparable to each other and agree with the original diagnosis of the genus, later slightly emended by Gründel and Nützel (2013). Therefore, in order to preserve the unambiguous identity of the genus and to ensure its nomenclatural stability the taxonomic species involved in the misidentification has been selected as the type species of *Camponaxis* in accordance with ICZN (1999) Art. 70.3.2. Therefore, *Camponaxis bandeli* sp. nov. is fixed as the new type species for *Camponaxis*. As a consequence, we have erected the new genus *Ederazyga* to include *C*.? *lateplicatum*.

The genus is close to *Stephanocosmia* Cossmann, 1895, and *Tyrsoecus* Kittl, 1892, in the presence of strong collabral ribs that are swollen on the peripheral belt. *Tyrsoecus* is smaller, more slender and with lower and more numerous whorls. *Stephanocosmia* lacks the spiral ornament and the collabral ribs attenuate and vanish on the last whorls where they reduce to a peripheral spiral row of nodes. Kaim et al. (2006) and Nützel et al. (2012) tentatively assigned to *Striazyga* Nützel, 1998, and *Katosira* Koken, 1892, some species here considered as belonging to *Ederazyga* (see list above). These genera differ from *Ederazyga* in having a turriculate shell of much smaller size, with less convex and lower whorls. Moreover, the collabral ribs are much less prominent and not swollen on the peripheral region.

The Early Jurassic genus *Pseudokatosira* Nützel and Gründel, 2007, is reminiscent of *Ederazyga* in the size and general characters of the shell, and in the presence of a distinct anterior canal. It differs in its more slender shell with less convex whorls. As detailed by Nützel and Gründel

(2007, 2015), in *Pseudokatosira* the collabral ribs of the early teleoconch attenuate after several whorls and then become broad, swollen on the periphery, on the last whorls. This ontogenetic change is absent in *Ederazyga*.

Ederazyga is also reminiscent of *Maturifusus* Szabó, 1983, type genus of the family Maturifusidae Gründel, 2001. The systematic position of this genus and of the family have been discussed by many authors (Szabó 1983; Bandel 1993, 2006; Schröder 1995; Gründel 1998, 1999, 2001, 2005; Riedel 2000; Guzhov 2004; Kaim 2004; Kaim and Beisel 2005; Nützel 2010; Bandel and Dockery 2012; Bouchet et al. 2017; Webster and Vermeij 2017). Most of them interpreted the Maturifusidae as a stem group of neogastropods or an ancient group of Latrogastropoda Riedel, 2000, probably close to the Buccinidae Rafinesque, 1815, or to the Purpurinidae Zittel, 1895. *Ederazyga* shares with *Maturifusus* the general shape of the shell, the peristome provided with an anterior opening and the strong ornament of spiral threads/cords overlapping collabral ribs. In *Ederazyga* the spire is more slender and the suture is more inclined. More relevant, the growth lines and, consequently, the collabral ribs are opisthocline and more distinctly parasigmoidal. About ten Jurassic species of *Maturifusus* have been described to date (Szabó 1983; Schröder 1995; Gründel 1998, 1999, 2001, 2005; Guzhov 2004; Kaim 2004) and all of them invariably show prosocline growth lines.

The same difference distinguishes *Ederazyga* from *Pseudotritonium* Wenz, 1940, a genus provisionally assigned by Nützel (2010) to the family Maturifusidae on the basis of its adult shell characters. Moreover, in *Pseudotritonium* the peristome is expanded on the outer lip. According to Nützel (2010), the affinities between *Pseudotritonium* and *Maturifusus*, if confirmed by the study of the protoconch, currently unknown in the type species of both genera, would indicate that the family Maturifusidae is a junior synonym of the family Pseudotritonidae Golikov and Starobogatov, 1987 (see also Bouchet et al. 2017).

Brachytrema? *despujolsi* Dubar, 1948, from the lower Pliensbachian of the High Atlas of Morocco (Dubar 1948: 62, pl. 3: 31–33), is similar to *Ederazyga* species in the general shape of the shell and in the ornament pattern with axial ribs that are swollen in the peripheral region. However, this species clearly belongs to a different genus in showing a markedly expanded aperture which is provided with a strong varix, and by prosocline collabral ribs and growth lines. In this respect, it seems more closely related to *Pseudotritonium*.

Obviously, the differential characters mentioned above, although suggesting closer relationships of *Ederazyga* with the Pseudozygopleuroidea Knight, 1930, are not sufficient to exclude the attribution of this genus to the Maturifusidae. A reliable and more precise taxonomic placement of *Ederazyga* requires information on its protoconch and on that of the other, comparable taxa.

The large shell, the pendent outline of the whorls and the opisthocline collabral ribs that are more prominent and swollen on the periphery make *Ederazyga* close to a group of currently unrevised *Zygopleura*-like species known especially from the Early Jurassic carbonate platforms of western Tethys. Since this group seemingly played an important role in the Early Jurassic gastropod recovery, comparisons with *Ederazyga* and a discussion of their possible evolutionary relationships are discussed below in the conclusion.

Stratigraphic and geographic range.—The genus ranges from the early Carnian to the late Rhaetian and its distribution extends from the Southern Alps to central Iran.

Ederazyga fanchini sp. nov.

Fig. 3.

Zoobank LSID: urn:lsid:zoobank.org:act:B3326419-D750-4FA6-8C62-984931816D37

Etymology: Species dedicated to Piero Fanchin, collaborator of MSNVI, who collected the material.

Holotype: MSNVI 042/049, internal and external moulds (Fig. 3A).

Type locality: Villa Edera section in Jadoul et al. (2005), southern side of Monte Tre Croci (Monte Campo dei Fiori group), Lombardy, northern Italy.

Type horizon: Upper Zu Limestone (sensu Jadoul et al. 2005), light nut-brown biocalcarenite, upper Rhaetian.

Material.—Type material and plaster cast replica of an internal mould MSNVI 042/049a (the original specimen has been lost).

Measurements.—Holotype MSNVI 042/049: height of the shell (not complete) 92.7 mm; height of the last whorl 58.1 mm; width of the shell 63.6 mm; apical angle 47°; pleural angle 50°. MSNVI 042/049a: height of the shell (not complete) 81.5 mm; height of the last whorl 67.1 mm; width of the shell 83.6 mm.

Diagnosis.—Shell moderately large, high-pagodiform and composed of about ten whorls. Height of last whorl slightly exceeding half-height of shell. Height of spire whorls about half of their width. Earliest teleoconch whorls regularly convex. Periphery of subsequent whorls slightly below mid-whorl surface. Peristome with wide anterior spout. Collabral ribs rather swollen on peripheral band and forming axially elongated nodes. Each whorl sculptured by 11 collabral ribs. Two orders of spiral threads on spire whorl. Up to four orders of spiral threads on last whorl.

Description.—The shell is large, pagodiform and composed of about ten whorls. The outline of the apical spire is almost conoid or feebly cyrtoconoid whereas the fully adult part of the shell is weakly coeloconoid. The spire whorls have a height slightly less than half of their width and the last whorl extends a little more than half of the shell height. The first two preserved teleoconch whorls appear regularly convex. On the subsequent whorls the periphery rapidly becomes prominent and corresponds to a rounded spiral belt where the axial ornament is rather strong. It lies slightly below mid-whorl and gives to the whorl surface an angular outline. The ramp is slightly concave whereas the surface below the periphery is convex and inclined towards the spire axis. The

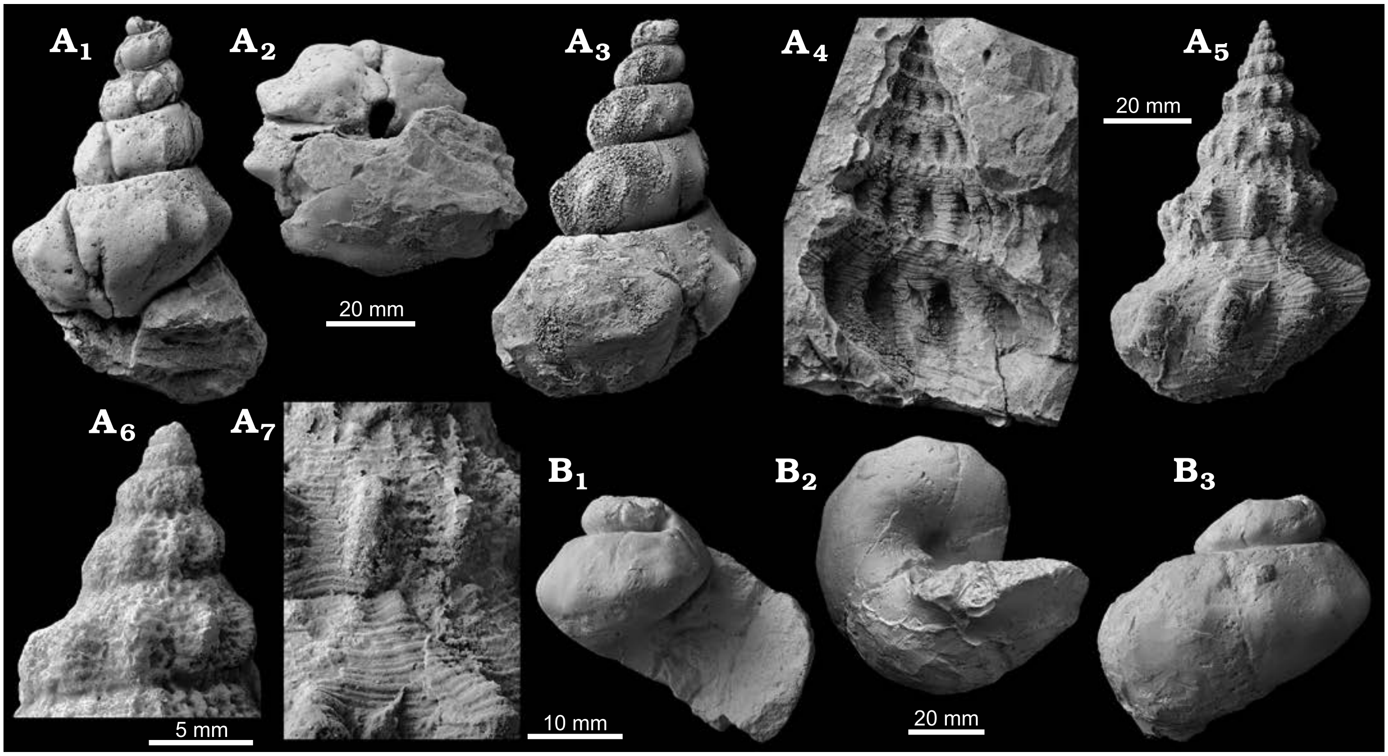

Fig. 3. Zygopleurid? gastropod *Ederazyga fanchini* gen. et sp. nov.; upper Rhaetian, Villa Edera (Lombardy, northern Italy). **A**. Holotype MSNVI 042/049, inner mould in apertural (A_1), basal (A_2), and dorsal (A_3) views; external mould in general view (A_4), rubber cast of the dorsal view (A_5), detail of the apical spire (A_6), and detail of the penultimate and last whorls (A_7). **B**. Plaster cast replica of MSNVI 042/049a, inner mould in apertural (B_1), basal (B_2), and dorsal (B_3) views.

suture is distinctly impressed, almost grooved. The base is subconoid with a moderately convex surface and most probably anomphalous. The aperture is drop-shaped tending to subpentagonal. The peristome at the junction of the basal lip with the columellar lip shows a short, low and wide anterior spout marked by the outward reflection of the shell surface. The teleoconch is ornamented by collabral ribs and spiral threads. Opisthocline and opisthocyrt collabral riblets and, seemingly, some spiral threads are visible at least on the second preserved whorl. On subsequent whorls the collabral riblets become strong ribs overlapped by cord-like spiral threads. On the fourth preserved whorl the collabral ribs are slightly opisthocline and extend from suture to suture. They are crossed by about six, equally spaced and sized cord-like threads that are slightly stronger when passing on the collabral ribs. The most adapical spiral thread bears a row of little nodes marking the abapical edge of the sutural groove (Fig. 3A_7). During the growth, the spiral threads increase in number by intercalation. Six primary spiral threads ornament the ramp of the penultimate whorl. They are intercalated by secondary threads running approximately along the mid-line of the intervals between the primary threads. The same number and pattern of spiral threads cover the remaining part of the whorl surface. Third and fourth orders threads appear sparsely on the last whorl making the spiral pattern less regular. The collabral ribs are rounded, widely spaced and opisthocline. They strengthen during growth and become rather prominent on the peripheral band where they form rounded and axially elongated nodes. On the ramp, the collabral ribs attenuate gradually towards the adapical suture whereas they keep their prominence on the outer face. Each whorl is sculptured by 11 collabral ribs which are not aligned axially with the ribs of the adjacent whorl and appear almost to alternate in position. The base is ornamented by the same spiral pattern as that of the whorl surface whereas the collabral ribs are weakly prosocyrt and seem to attenuate towards the axial region. The whorl surface is crossed by opisthocline and feebly opisthocyrt growth lines, slightly prosocyrt on the subsutural band. On the last whorl, the growth lines occasionally form irregular collabral thickenings that are more marked on the ramp. Although the growth lines are not clearly identifiable on the basal surface, the shape of the collabral ribs and traces of growth thickenings indicate that they are prosocyrt.

Remarks.—The holotype is represented by an external mould and internal mould. The external mould preserves only part of the base which seems to be anomphalous. The internal mould lacks the apical spire and shows a deep axial cavity presumably reflecting the presence of a smooth and robust columella. The aperture is incomplete. Its shape and the morphology of the base indicate that the columellar lip is slightly downward elongated in the axial direction. On the other available specimen (MSNVI 042/049a), which is represented by the plaster cast replica of an internal mould, the junction of the columellar lip with the basal lip is outwardly reflected. Here the basal lip, though incomplete, forms an evident curve reflecting the presence of a short and wide anterior spout (Fig. 3B_2, B_3). The external mould of the holotype shows details of the ornament and the apical spire. These characters are well reproduced on its rubber cast. The apical spire is almost complete but poorly preserved.

Ederazyga lateplicata (Klipstein, 1843) and the specimen assigned by Nützel et al. (2012) to the same species differ from *Ederazyga fanchini* sp. nov. in their smaller size. The shells are more slender and fusiform and the whorls are higher. Moreover, the holotype of *E. lateplicata* shows sharper collabral ribs, with a less swollen periphery, and a distinct anterior canal on the peristome. *Striazyga*? sp. described by Kaim et al. (2006), here considered as belonging to *Ederazyga*, is more slender and acute. Moreover, the whorls are more regularly convex, the collabral ribs are slightly more numerous and the spiral ornament is less sharp.

Stratigraphic and geographic range.—Type locality and horizon only.

Ederazyga lateplicata (Klipstein, 1843) comb. nov.

Figs. 2A, 4.

1843 *Cerithium* (?) *lateplicatum* n. sp.; Klipstein 1843: 182, pl. 11: 35.

?1868 *Loxonema lateplicata* Klipstein, 1845 (sic!); Laube 1868: 62–63, non pl. 24: 14.

1894 *Katosira* (?) *lateplicata* Klipstein, 1843 (sic!); Kittl 1894: 164–165, pl. 4: 27–28.

?1978 *Katosira seelandica* (Kittl, 1894) var. *alta* n.f.; Zardini 1978: 43–44, pl. 28: 8a, b.

non1995 *Camponaxis lateplicata* (Klipstein, 1843); Bandel 1995: 27, pl. 13: 9, pl. 14: 1–5.

non2012 *Katosira*? *lateplicata* (Klipstein, 1843); Nützel et al. 2012: 56, fig. 3G.

Material.—A single specimen (NHMUK PI OR 35701) is present in the Klipstein's collection of the NHMUK. It corresponds to the single shell figured by Klipstein (1843: pl. 11: 35) and therefore it is deemed to be the holotype of the species. Saint Cassian Formation, lower Carnian, Kreutzkofel (eastern Dolomites, northern Italy).

Measurements.—Height of the shell (not complete) 28.0 mm; apparent width of the shell 17.8 mm; height of last whorl 21.1 mm; apparent pleural angle 31°.

Description.—The shell is slender, seemingly fusiform-turriculate. The whorls are strongly convex, with a roundedly prominent periphery at their mid-line. The periphery tends to become subangulate on the last whorl. The surface of the

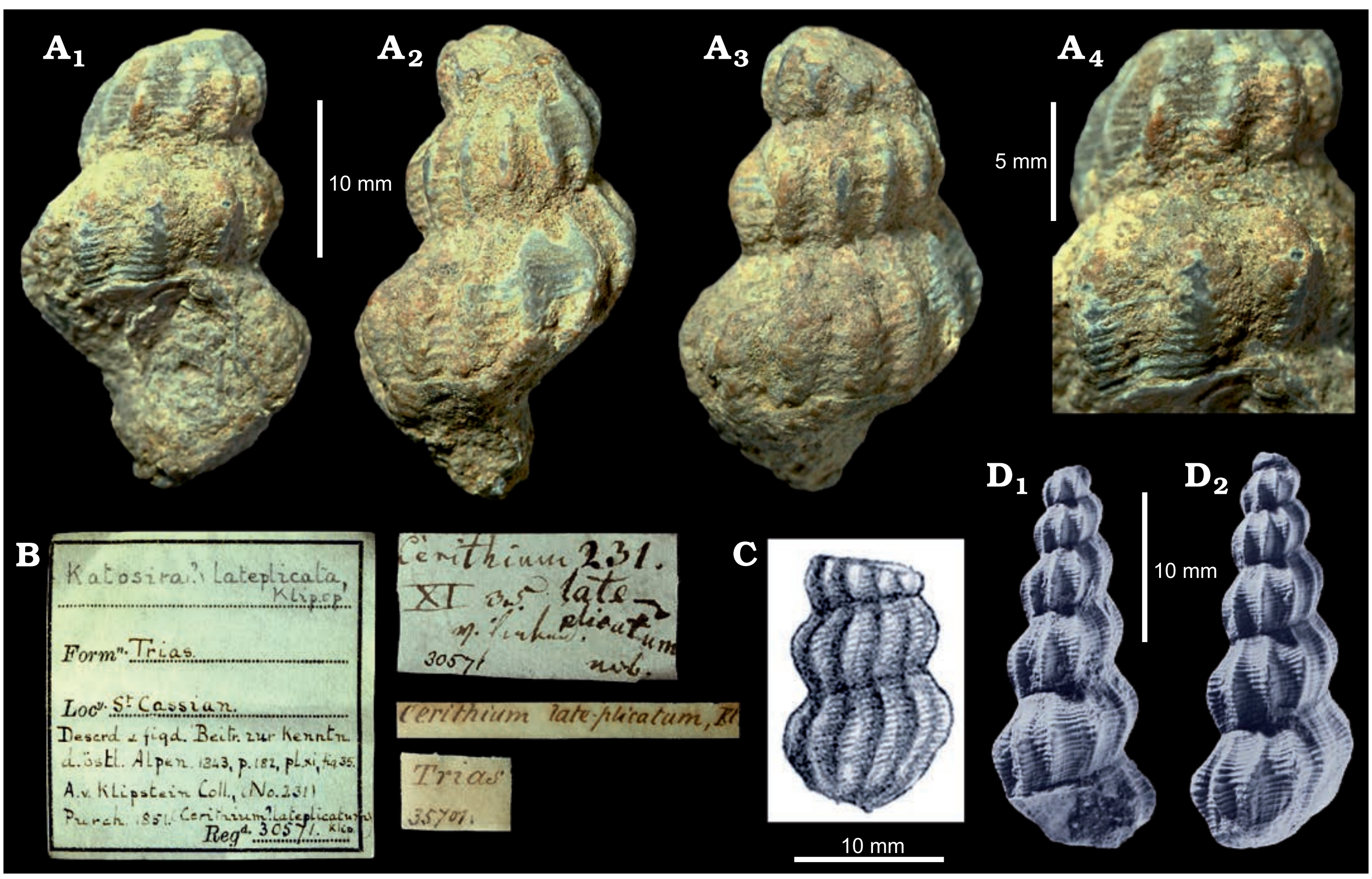

Fig. 4. Zygopleurid? gastropod *Ederazyga lateplicata* (Klipstein, 1843); lower Carnian, eastern Dolomites (Southern Alps, northern Italy). **A**. Holotype NHMUK PI OR 35701, incomplete shell, in apertural (A_1), dorsal (A_2), and subdorsal (A_3) views, detail of the ornament (A_4). **B**. Original labels of the holotype (the label at the top shows an incorrect inventory number). **C**. Illustration of a specimen classified by Kittl (1894: pl. 4: 28) as *Katosira*? *lateplicata*. **D**. Original illustration of the specimen MRZ3711, ascribed by Zardini (1978: pl. 28: 8a, b) to *Katosira seelandica* var. *alta*, incomplete shell, in apertural (D_1) and dorsal (D_2) views, reproduced with permission Tipografia Ghedina Snc.

whorl is slightly concave below the suture. The width of the penultimate whorl is two times its height and the last whorl is seemingly half the reconstructed height of the shell. The base is anomphalous, conoidal and downward elongated to form a lower neck. The surface of the base is evenly convex and passes smoothly to the whorl side. The peristome is not preserved but the cross section of the last whorl indicates a seemingly ovoid and axially elongated aperture. The columella is stout and straight. It extends downward in axial direction where edges a distinct lower canal. The collabral ornament consists of strong and gently opisthocline ribs. They are moderately swollen on the peripheral region and become thinner towards both the sutures. The penultimate whorl bears about ten ribs. Dense, sharp, subequally spaced and sized spiral threads overlap the collabral ribs. An alternation of finer and coarser spiral threads is visible in a wide area above and below the periphery. The finer threads are about half the width of the coarser ones and possibly occur also in the other parts of the shell. On the ribs, the spiral threads become slightly thicker and seem to form low, spirally elongated nodes. About fifteen spiral threads ornament the penultimate whorl.

Remarks.—The specimen preserves only the last two whorls and it is slightly deformed by compaction. Thought incomplete, the peristome shows the presence of a distinct lower canal. Since the surface of the shell is partly covered by a hard matrix, the details of the ornament, especially the finer spiral threads, are visible only in patches. Most probably the material on which Zardini (1978) (Fig. 4D) instituted *Katosira seelandica* var. *alta* Zardini, 1978, belongs to *Ederazyga lateplicata* (Klipstein, 1843). It differs only in the slightly higher whorls and less numerous collabral ribs. As reported by Kittl (1894), the illustration of the shell ascribed by Laube (1868) to *Loxonema lateplicata* is a composite from fragmentary specimens belonging to different species. According to him, the most complete specimen belongs to *Coronaria subcompressa* Kittl, 1894, whereas other two specimens most probably belong to *Katosira*? *lateplicata*. Nützel et al. (2012) also maintained that Laube (1868) illustrated a shell different from Klipstein's (1843) holotype. The specimen from the middle Norian beds of Nayband Formation (central Iran) assigned by Nützel et al. (2012) to *K*.? *lateplicata* represents a different and probably new species. Although clearly congeneric, this species differs from *E. lateplicata* in its more angular and pendent whorls, and in the collabral ribs that are more swollen and less numerous.

Stratigraphic and geographic range.—Lower Carnian, eastern Dolomites, northern Italy.

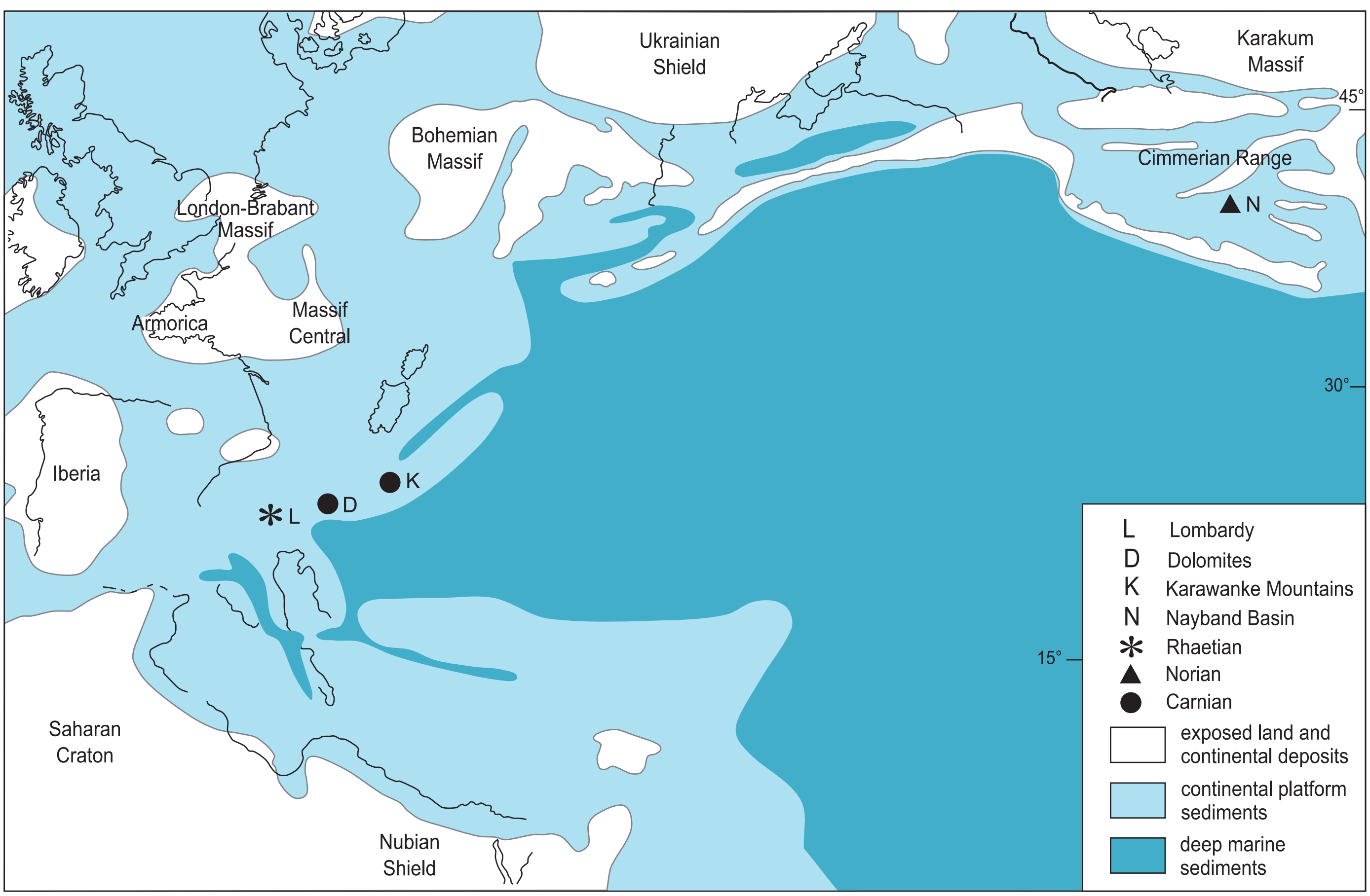

Fig. 5. Palaeogeographical distribution of *Ederazyga* during the Late Triassic. Map modified from the late Norian maps of Dercourt et al. (2000) and Barrier and Vrielinck (2008).

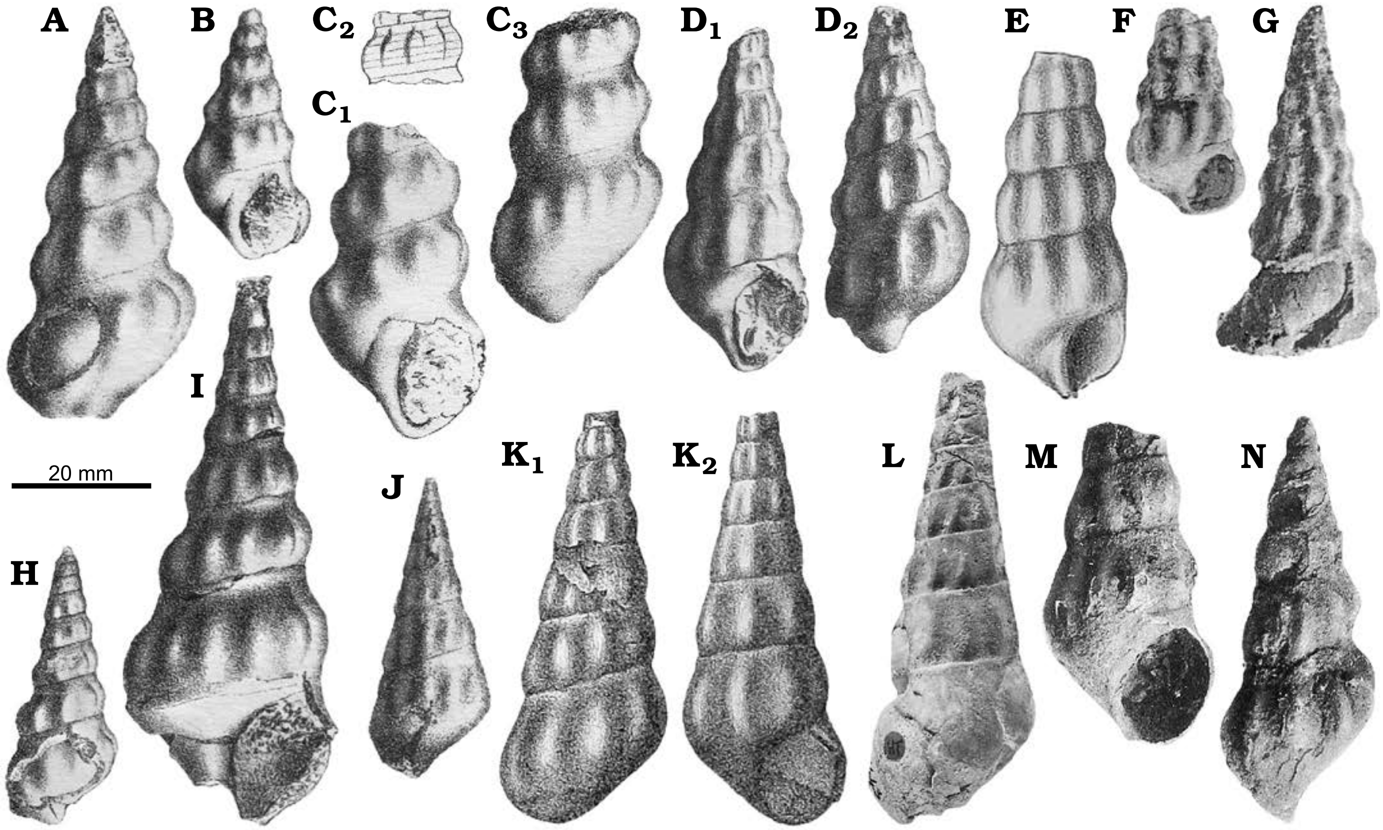

Fig. 6. Original illustrations of the Early Jurassic *Zygopleura*-like species probably closely related to *Ederazyga*. **A**, **B**. *Chemnitzia moorei* Gemmellaro, 1878 (pl. 6: 4, 5), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy). **C**. *Chemnitzia tatia* Gemmellaro, 1878 (pl. 6: 1–3), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy), in apertural view (C_1), detail showing the spiral ornament (C_2), and dorsal view (C_3). **D**. *Chemnitzia polyplecta* Gemmellaro, 1878 (pl. 6: 7, 8), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy), in apertural (D_1) and dorsal (D_2) views. **E**. *Chemnitzia catacyclus* Di Stefano, 1887 (pl. 2: 7b), Sinemurian, Taormina (eastern Sicily, southern Italy). **F**, **G**. Specimens figured by Dubar (1948: pl. 7: 11a, 12) as *Zygopleura paradisi* (Böhm, 1884), lower Pliensbachian (F) and lower Toarcian (G), Djebel Bou-Dahar, (High Atlas, Morocco). **H**, **I**. *Chemnitzia appenninica* Gemmellaro, 1878 (pl. 9: 1, 2), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy). **J**. *Chemnitzia veturia* Gemmellaro, 1878 (pl. 6: 6), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy). **K**. Specimen figured by Fucini (1895: pl. 12: 5, 5a) as *Zygopleura polyplecta* (Gemmellaro, 1878), Sinemurian, Monte Pisano (Tuscany, central Italy). **L**. *Zygopleura subnodosa* (d'Orbigny, 1850), holotype figured by Fischer and Weber (1997: pl. 1: 8), upper Pliensbachian, Calvados (northern France), in dorsal (K_1) and apertural (K_2) views. **M**, **N**. *Zygopleura vinosimonensis* Fischer and Weber, 1997, syntypes figured by Cossmann (1902: pl. 4: 2, 4) as *Zygopleura subnodosa*, Hettangian, Vendée (western France).

Discussion

Palaeobiogeography.—Occurrences of *Ederazyga* species are sparse and far apart (Fig. 5). Their rather patchy palaeogeographical distribution could reflect a primary rarity of the taxon in Late Triassic gastropod communities. However, the bias of preservation probably played a role especially in the Norian–Rhaetian record of the carbonate platform units. The genus ranges from Carnian to Rhaetian and its palaeogeographical distribution extends from the Southern Alps to central Iran. In the Southern Alps *Ederazyga* first occurs in the lower Carnian beds of the St. Cassian Formation with *Ederazyga lateplicata*. The genus is also present in the middle–upper part of the Carnian (post-Cordevolian in a tripartite scheme of the Carnian stage) of the Karavanke Mountains (Slovenia) (*Striazyga*? sp. in Kaim et al. 2006). The data presented here indicate that in the Southern Alps *Ederazyga* persisted up to the late Rhaetian.

The occurrence of *Ederazyga* in the Norian beds of the Nayband Basin (central Iran) (*Katosira*? *lateplicata* sensu Nützel et al. 2012) suggests an eastward extension of its distribution during that time. The Nayband Basin originated during the Eo-Cimmerian phase of collision of the Iran plate with the Turan plate (Eurasia) (Fürsich et al. 2005; Barrier and Vrielinck 2008; Brunet et al. 2009; Wilmsen et al. 2009). According to Wilmsen et al. (2009), its formation was the consequence of the onset of subduction of the Neotethys at the southern margin of the Iran plate in middle Norian times. The benthic macrofaunas of the Nayband Basin show affinities with those of both the Alpine region and south-eastern Asia (Fürsich et al. 2005 and references therein). *Ederazyga* could be interpreted as one of the Alpine gastropod taxa appearing in this area after the formation of the basin. The close relationships highlighted by Nützel and Senowbari-Daryan (1999), at least at the genus rank, between some of the Norian–Rhaetian gastropods of the Nayband Basin and

Table 1. List, references, localities, and stratigraphical position of the Early Jurassic *Zygopleura*-like species possibly related to *Ederazyga*.

Species	Localities	Stratigraphical levels	References
Zygopleura vinosimonensis Fischer and Weber, 1997	Vendée (western France)	Hettangian	Fischer and Weber 1997: 16; Cossmann 1902: 189, pl. 4: 2, 4, described as *Zygopleura subnodosa*; Cossmann 1913: 186, pl. 10: 4, 5, described as *Zygopleura subnodosa*
Melania theodori Terquem, 1855	Lorraine (eastern France)	upper Hettangian	Terquem 1855: 257, pl. 14: 6, 6a
	southern Luxembourg	upper Hettangian	Meier and Meiers 1988: 40, pl. 9: 25a, b, described as *Zygopleura etalensis*; SM, personal observation 2019
Zygopleura subnodosa (d'Orbigny, 1850)	Calvados (northern France)	upper Pliensbachian	Eudes-Deslongchamps 1843: 219, pl. 12: 1, described as *Melania nodosa*; d'Orbigny 1850: 226; d'Orbigny 1851: 37, pl. 237bis: 6; Fischer and Weber 1997: 15, pl. 1: 8
Chemnitzia tatia Gemmellaro, 1878	north-western Sicily (southern Italy)	Sinemurian	Gemmellaro 1878: 135, pl. 6: 1–3; De Gregorio 1886: 6
	eastern Sicily (southern Italy)	Sinemurian	Di Stefano 1887: 431, pl. 2: 6a, b
	Tuscany (central Italy)	Sinemurian	Fucini 1895: 315
	eastern High Atlas (Morocco)	?Sinemurian (Dresnay 1966)	?Bourrouilh 1966: 45, pl. 1: 6a, b, described as *Zygopleura subnodosa*
Chemnitzia polyplecta Gemmellaro, 1878	north-western Sicily (southern Italy)	Sinemurian	Gemmellaro 1878: 137, pl. 6: 7, 8
	eastern Sicily (southern Italy)	Sinemurian	Di Stefano 1887: 432, pl. 2: 11, 12
	Tuscany (central Italy)	Sinemurian	Fucini 1895: 316, pl. 12: 5, 5a
	Trento Platform (northern Italy)	Pliensbachian	Dal Piaz 1909: 9, pl. without number: 8, 9
Chemnitzia moorei Gemmellaro, 1878	north-western Sicily (southern Italy)	Sinemurian	Gemmellaro 1878: 136, pl. 6: 4, 5
	Tuscany (central Italy)	Sinemurian	Fucini 1895: 317
Chemnitzia veturia Gemmellaro, 1878	north-western Sicily (southern Italy)	Sinemurian	Gemmellaro 1878: 139, pl. 6: 6
	Tuscany (central Italy)	Sinemurian	Fucini 1895: 319, pl. 12: 12, 12a
Chemnitzia catacyclus Di Stefano, 1887	eastern Sicily (southern Italy)	Sinemurian	Di Stefano 1887: 432, pl. 2: 7, 8
Chemnitzia appenninica Gemmellaro, 1878	north-western Sicily (southern Italy)	Sinemurian	Gemmellaro 1878: 138, pl. 6: 10, pl. 9: 1, 2
	High Atlas (Morocco)	lower Pliensbachian	Dubar 1948: 98, pl . 9: 1a, b
Chemnitzia paradisi Böhm, 1884	Trento Platform (northern Italy)	Pliensbachian	Böhm, 1884: 782, pl. 26: 5
	High Atlas (Morocco)	lower Pliensbachian and lower Toarcian	Dubar 1948: 99, pl. 7: 11, 12

the older, mainly Carnian fauna of the Southern Alps seems to support this suggestion.

Relationships with the Early Jurassic gastropods.—The stratigraphical distribution of *Ederazyga* does not cross the Triassic/Jurassic boundary. In fact, the genus is absent from the well documented earliest Jurassic gastropod faunas of Europe (see Monari et al. 2011 for references). Its last occurrence, i.e., *E. fanchini*, is only a few meters below the stratigraphical discontinuity that, according to Jadoul et al. (2005) marks the Triassic/Jurassic boundary in western Lombardy.

A number of Early Jurassic species, namely *Chemnitzia tatia* Gemmellaro, 1878, *Chemnitzia polyplecta* Gemmellaro, 1878, *Chemnitzia moorei* Gemmellaro, 1878, *Chemnitzia appenninica* Gemmellaro, 1878, *Chemnitzia veturia* Gemmellaro, 1878, *Chemnitzia catacyclus* Di Stefano, 1887, and *Chemnitzia paradisi* Boehm, 1884 (Table 1, Fig. 6A–K; see also Gatto and Monari 2010), share with *Ederazyga* the shape and the medium to large size of the shell, the outline of the whorls and the ornament of strong, opisthocline collabral ribs that are swollen or subnodose in the peripheral region. The only appreciable difference is their lack of a prominent spiral ornament. These species are reported only in very old literature sources or have been no longer quoted after their initial description, and revision probably will lead to the reduction of their number. In any case, they occur frequently in the Sinemurian–Pliensbachian carbonate platform deposits of the Mediterranean region, such as those of the Trapanese Platform (north-western Sicily, southern Italy), the Longi-Taormina unit of the Calabrian Arc (eastern Sicily, southern Italy), the Tuscany Zone (central Italy), the Trento Platform (northern Italy) and the High Atlas (Morocco) (Fig. 7).

Species showing the same characters are known also from the Hettangian–Pliensbachian epicontinental deposits of the Paris Basin and Vendée (eastern France), namely *Zygopleura subnodosa* (d'Orbigny, 1850), *Zygopleura vinosimonensis* Fischer and Weber, 1997, and *Melania theodori* Terquem, 1855 (Table 1, Figs. 6L–N, 7). According to Cossmann (1907), *Z. subnodosa*, together with *Zygopleura*? *benoisti* Cossmann, 1907, a species from the Bathonian of the Paris Basin (Cossmann 1907; Fischer 1964), differs from the typical Triassic representatives of *Zygopleura* Koken, 1892, in having a much bigger shell ornamented by collabral ribs that are swollen or subnodose on the peripheral region. In his opinion, they probably belong to a distinct Jurassic genus. This suggestion is plausible if one considers the clear

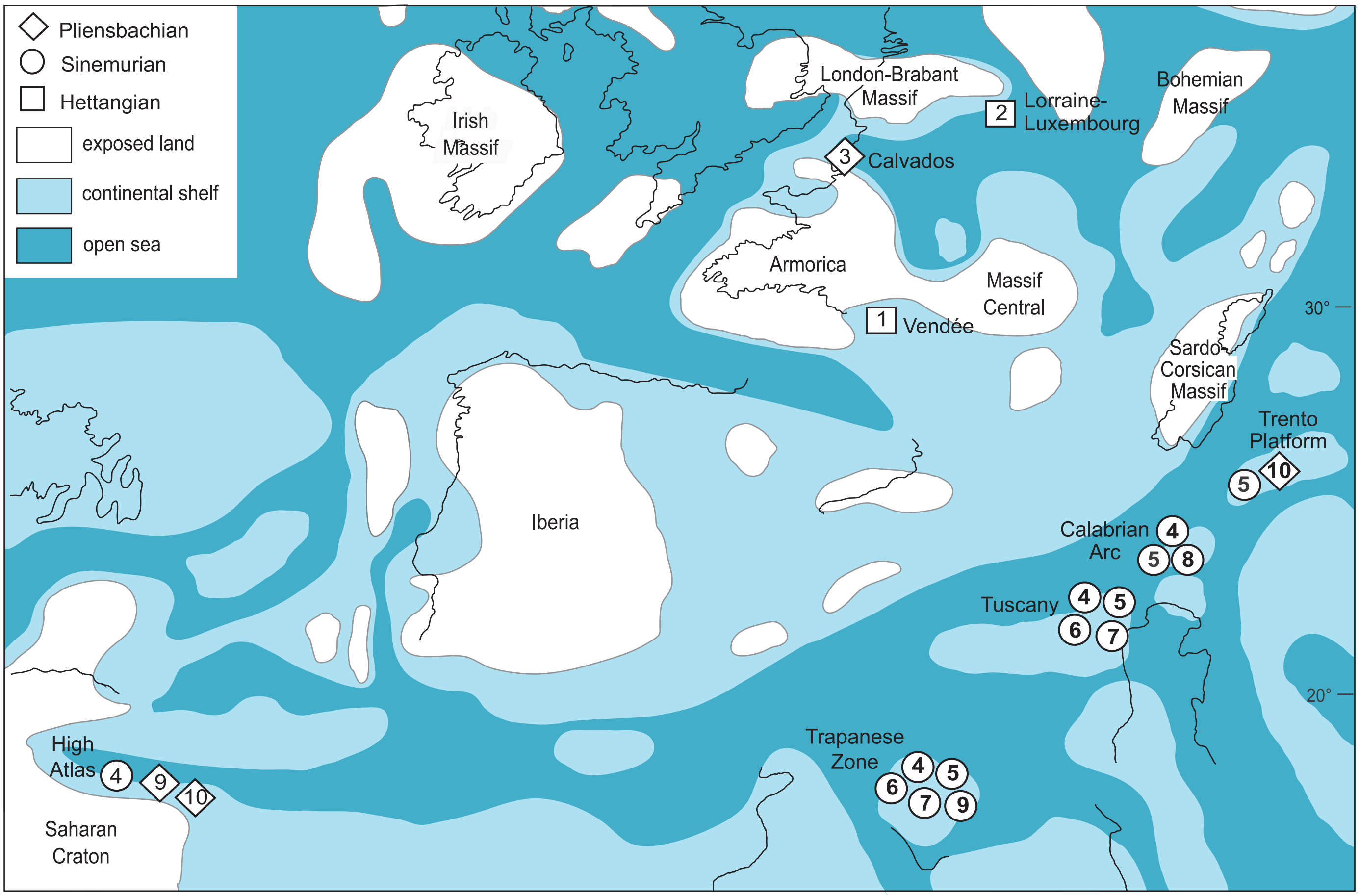

Fig. 7. Early Jurassic palaeogeographical distribution of the *Zygopleura*-like species listed in Table 1. Map simplified from the late Sinemurian map of Dercourt et al. (2000). Abbreviations: 1, *Zygopleura vinosimonensis*; 2, *Melania theodori*; 3, *Zygopleura subnodosa*; 4,*Chemnitzia tatia*; 5, *Chemnitzia polyplecta*; 6, *Chemnitzia moorei*; 7, *Chemnitzia veturia*; 8, *Chemnitzia catacyclus*; 9,*Chemnitzia appenninica*; 10, *Chemnitzia paradisi*.

uniformity of the adult characters of these species and of those listed above from the Mediterranean region. However, a confirmation needs the study of their protoconchs, that are currently unknown. Since also *Ederazyga* lacks information on the protoconch, its relationships with this group of species cannot be fully established and remain a matter for future researches. At the present, based on the available teleoconch characters, one cannot exclude that *Ederazyga* represents a Triassic member of a group that during the Early Jurassic radiated both in the western Tethyan carbonate platforms and in the European epicontinental shelf, testifying to the gastropod recovery after the Late Triassic decline in biodiversity.

Conclusions

The Late Triassic gastropod record shows a strong and progressive post-Carnian loss of species richness that most probably reflects a real decrease of overall diversity. For this reason, the Rhaetian record is in general rather poor. As far as the Alpine region is concerned, its interpretation is particularly problematic because, in addition to the scarcity of data, the literature sources (see references cited above) are significantly outdated and, in most cases, the gastropod faunas are poorly preserved. However, the present day knowledge of the systematics of the class Gastropoda is incomparably better than in the past, mainly thanks to the numerous contributions made in the last few decades (see Bouchet and Rocroi 2005 and Bouchet et al. 2017 for references). In this context, the work presented here can be regarded as a case study demonstrating that a systematic analysis can allow us to gain useful morphological information even from the study of incomplete and poorly preserved material. On the other hand, the study shows the main constraints imposed by the preservation of the material. They are mostly due to the lack of the protoconch, making uncertain the suprageneric attribution of *Ederazyga* and, therefore, its systematic relationships with other comparable taxa. However, one should underline that, since the protoconch is frequently not preserved, these uncertainties are common also to many other gastropod faunas represented by better preserved and richer material.

From a preliminary estimate, about 70 species were so far identified from the Rhaetian deposits of the Alpine region, and numerous other species were quoted in open nomenclature. In the light of this study, it seems highly likely that their revision would add important data permitting us to better understand the reasons for the impoverishment of the Late Triassic gastropod record in the Alpine region and to better assess the faunal turnover related to the subsequent Early Jurassic recovery.

Acknowledgements

We thank Piero Fanchin (Cassano Magnago, Varese, Italy), collaborator of the MSNVI for allowing access to the material studied here and for the geographical and stratigraphical information on its finding. We are also indebted to Flavio Jadoul (University of Milan, Italy) for additional data on the stratigraphy of the type locality, Roberto Gatto (University of Padua, Italy) for his critical reading of an earlier version of the paper. Alexander Nützel (Bayerische Staatssammlung für Paläontologie und Geologie and Ludwig Maximilian University, Münich, Germany) kindly provided further information on *Cerithium*? *lateplicatum*. Mariel Ferrari (Instituto Patagónico de Geología y Paleontología, Puerto Madryn, Argentina) and Alexander Nützel are acknowledged for their constructive reviews. The photographic work has been executed by Stefano Castelli and the line drawings by Nicola Michelon (both University of Padua, Italy). The paper was supported by the fund GATT-SID17-01-2017 of the University of Padua.

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