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New hexapodid crabs from the Eocene of Vicenza (NE Italy) (Crustacea, Decapoda, Brachyura, Hexapodidae)

Abstract - The Hexapodidae was known to date from the Cenozoic of Veneto by *Steeva cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, from the middle Eocene of Chiampo Valley (Vicenza), and *Palaeopinnixa* sp. from the upper Eocene of Possagno (Treviso). Recent discoveries from the Eocene of Vicenza area allowed to describe three new genera and four new species of hexapodids. *Bellhexapus granulatus* n. gen., n. sp., *Eohexapus albertii* n. gen., n. sp., and *Eurohexapus lobatus* n. gen., n. sp. from the middle Eocene of "Albanello" quarry at Nogarole Vicentino (Vicenza), and *Palaeopinnixa alontensis* n. sp. from the upper Eocene of Alonte (Vicenza). *Bellhexapus granulatus* n. gen., n. sp. and *Eurohexapus lobatus* n. gen., n. sp. preserve the carapace, the ventral and abdominal male parts, while *Eohexapus albertii* n. gen., n. sp. preserves the carapace, the ventral and abdominal female parts. *Palaeopinnixa alontensis* n. sp. preserves instead only the carapace.

Key words: Crustacea, Decapoda, Hexapodidae, Eocene, NE Italy.

Riassunto - Nuovi crostacei hexapodidi dell'Eocene di Vicenza (NE Italia) (Crustacea, Decapoda, Brachyura, Hexapodidae).

La famiglia Hexapodidae era finora conosciuta nel Terziario del Veneto con *Steeva cesarii* Beschin, Busulini, De Angeli & Tessier, 1994 dell'Eocene medio della Valle del Chiampo (Vicenza) e *Palaeopinnixa* sp. dell'Eocene superiore di Possagno (Treviso). Recenti ritrovamenti nelle rocce eoceniche del Vicentino hanno permesso di descrivere tre nuovi generi e quattro nuove specie di hexapodidi. *Bellhexapus granulatus* n. gen., n. sp., *Eohexapus albertii* n. gen., n. sp. e *Eurohexapus lobatus* n. gen., n. sp. provengono dalle marne vulcanodetritiche dell'Eocene medio di Cava "Albanello" di Nogarole Vicentino (Vicenza) e *Palaeopinnixa alontensis* n. sp. è stata rinvenuta in calcareniti dell'Eocene superiore di Alonte (Vicenza). *Bellhexapus granulatus* n. gen., n. sp. e *Eurohexapus lobatus* n. gen., n. sp. oltre al carapace, conservano le parti ventrali ed addominali maschili, mentre *Eohexapus albertii* n. gen., n. sp. oltre al carapace, conserva le parti ventrali ed addominali femminili. *Palaeopinnixa alontensis* n. sp. conserva invece solo il carapace.

Parole chiave: Crustacea, Decapoda, Hexapodidae, Eocene, Italia settentrionale.

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Introduction and geological setting

The hexapodids can be easily distinguished from the other brachyurans by having only four pairs of pereopods (the last pereopod shows only a vestigial coxa) instead of five and similarly developed sternites 5-7 and an extremely reduced sternite 8, may be completely concealed under the carapace. The family is represented by a small number of both fossil and extant species, widespread from the Late Cretaceous to Recent.

The fossil species known to date in Veneto (NE Italy) were *Stevea cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, from the middle Eocene (middle Lutetian) of “Albanello” quarry at Nogarole Vicentino (Vicenza), and *Palaeopinnixa* sp. reported by Busulini & Beschin (2009) from the upper Eocene of Possagno (Treviso).

The re-examination of the holotype of *Stevea cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, by Guinot *et al.* (in press) and the study of newly collected fossil material have pointed out that several morphological characters are different from those of the type species *Stevea williamsi* (Glassell, 1938). In one specimen of the type sample (MCZ 1430), studied by Beschin *et al.* (1994: Pl. 10, fig. 2) from the middle Eocene (lower Lutetian) of “Boschetto” quarry at Nogarole Vicentino, the carapace is wider than long and the ratio length/width (0.62) is lower than that (0.72) of the holotype of *S. cesarii*. Moreover, the specimen has weak branchio-cardiac grooves, wider orbits, and sinuous supraorbital margins. Consequently this specimen cannot be ascribed to *S. cesarii*. Finally, *Palaeopinnixa* sp. described by an inner cast of carapace by Busulini & Beschin (2009: 116, figs. 9, 10) must be assigned to *P. alontensis* n. sp.

The specimens studied here come from two different areas of Vicenza province: Eastern Monti Lessini (“Albanello” quarry at Nogarole Vicentino) and Monti Berici (Alonte) (Fig. 1).

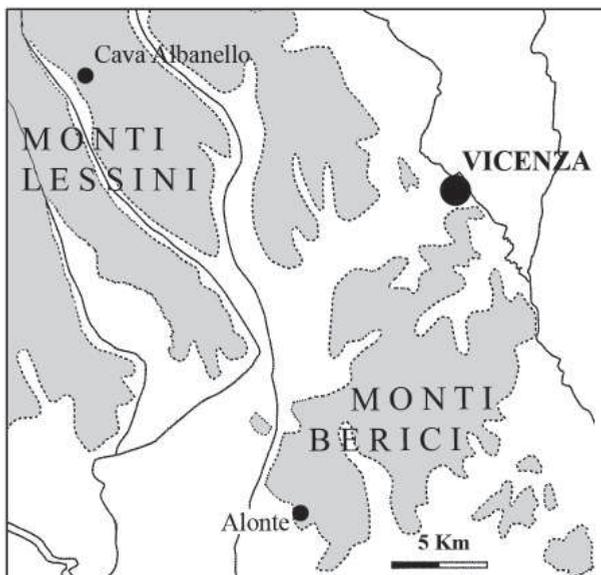


Fig. 1 - Geographic map of Vicenza area with the fossiliferous localities (mappa del territorio Vicentino con le località fossilifere).

The “Albanello” quarry, now inactive, is located on the left side of the Chiampo Valley. The stratigraphic sequence is represented by Eocene calcarenitic layers intercalated with volcanic materials staying on Scaglia Rossa from the Late Cretaceous (De Zanche, 1965). The “Albanello” quarry has the same stratigraphic section of the “Boschetto” quarry at Nogarole Vicentino, studied by Ungaro *in* Beschin *et al.* (1991). The volcanodetritic marls, preserving the decapod crustaceans, have been ascribed to the high part of the lower Lutetian (*Nummulites obesus* Zone) and to the lower part of the middle Lutetian (*Nummulites beneharnensis* Zone). The decapod crustaceans of “Albanello” quarry have been the subjects of many studies (Beschlin *et al.*, 1994, 2001; Beschlin & De Angeli, 2004; De Angeli & Beschlin, 2006, 2007).

Alonte is located on the SW side of Monti Berici. The decapod crustaceans were discovered in the quarry located N of Alonte. They were discovered in a well stratified biocalcarenic layers, preserving also many inner casts of molluscs and corals. The study of the stratigraphic sequence by the nannofossil analysis has established an upper Eocene age (Beccaro pers. com., 2003).

Material

The studied sample includes sixteen specimens of hexapodid crabs housed in the Museo Civico “G. Zannato”, Montecchio Maggiore (Vicenza) (MCZ) and in the Museo di Storia Naturale, Milano (MSNM). The specimens are three-dimensionally preserved within a volcanodetritic marl from the middle Eocene and within a calcarenitic rock from the upper Eocene. The studied specimens have been ascribed to *Bellhexapus granulatus* n. gen., n. sp. (two specimens), *Eohexapus albertii* n. gen., n. sp. (three specimens), *Eurohexapus lobatus* n. gen., n. sp. (three specimens), and *Palaeopinnixa alontensis* n. sp. (eight specimens).

Measurements are given in millimetres (mm).

The systematic arrangement used in this paper follows the recent classification proposed by Ng *et al.* (2008) and De Grave *et al.* (2009).

Abbreviations

cl: carapace length; cw: carapace width; wo-f: width of orbito-frontal margin; wf: width of frontal margin; mxp3: third maxilliped; P2: second pereopod; P4: fourth pereopod; P5: fifth pereopod.

Systematic Palaeontology

Infraorder Brachyura Linnaeus, 1758
 Eubrachyura Saint Laurent, 1980
 Heterotremata Guinot, 1977
 Superfamily Hexapodoidea Miers, 1886
 Family Hexapodidae Miers, 1886

Discussion. The taxonomy of the Hexapodidae Miers, 1886, has been revised by Manning & Holtuis (1981). The morphological characters of the family have been discussed by Guinot (1978, 1979, 2006), Guinot & Bouchard (1998), Ng (1998), Schweitzer & Feldmann (2001), and Huang *et al.* (2002).

The Hexapodidae Miers, 1886, comprises fossil and extant genera as follows:

Bellhexapus n. gen. – includes only the type species *B. granulatus* n. sp. (fossil).

Eohexapus n. gen. – includes only the type species *E. albertii* n. sp. (fossil).

Eurohexapus n. gen. – includes only the type species *E. lobatus* n. sp. (fossil).

Goniocypoda Woodward, 1867 – includes the type species *G. edwardsi* Woodward, 1867 (fossil); *G. collinsi* Crane & Quayle, 1986 (fossil); *G. elmorensis* Crane & Quayle, 1986 (fossil); *G. quaylei* Crane, 1981 (fossil); *G. rajasthanica* Glaessner & Rao, 1960 (fossil); *G. sindensis* Glaessner, 1933 (fossil); *G. sulcata* Carter, 1898 (fossil); *G. tessieri* Remy in Remy & Tessier, 1954 (fossil); *G. transilvanica* Bittner, 1893 (fossil); and *G. verheyeni* Fraaije, van Bakel & Jagt, 2007 (fossil).

Hexalaghlia Guinot, 2006 – includes the type species *H. orientalis* (Rathbun, 1909, as *Thaumastoplax*) (extant) and *H. kuenensis* (Rathbun, 1909, as *Thaumastoplax*) (extant).

Hexapinus Manning & Holthuis, 1981 – includes the type species *H. latipes* (De Haan, 1835, as *Hexapus*) (extant); *H. buchanani* (Monod, 1956, as *Hexapus*) (extant); and *H. granuliferus* (Campbell & Stephenson, 1970, as *Hexapus*) (extant).

Hexaplax Doflein, 1904 – includes only the type species *H. megalops* Doflein, 1904 (extant).

Hexapus De Haan, 1833 – includes the type species *H. sexpes* (Fabricius, 1798, as *Cancer*) (extant); *H. anfractus* (Rathbun, 1909, as *Lambdophallus*) (fossil and extant); *H. decapoda* (Morris & Collins, 1991, as *Prepaeduma*) (fossil); ?*H. edwardsi* Serène & Soh, 1976 (extant); *H. estuarinus* Sankarankutty, 1975 (extant); *H. granuliformis* Karasawa & Kato, 2008 (fossil); *H. nakajimai* Imaizumi, 1959 (fossil); *H. pinfoldi* Collins & Morris, 1978 (fossil); and *H. stebbingi* Barnard, 1947 (extant).

Lambdophallus Alcock, 1900 – includes only the type species *L. sexpes* Alcock, 1900 (extant).

Latohexapus Huang, Hsueh & Ng, 2002 – includes only the type species *L. granosus* Huang, Hsueh & Ng, 2002 (extant).

Paeduma Rathbun, 1897 – includes only the type species *P. cylindracea* (Bell, 1859, as *Amorphopus*) (extant).

Palaeopinnixa Vía Boada, 1966 – includes the type species *P. rathbunae* Schweitzer, Feldmann, Tucker & Berglund, 2000 (fossil); *P. alontensis* n. sp. (fossil); *P. eocenica* (Woods, 1922, as *Thaumastoplax*) (fossil); *P. granulosa* Schweitzer & Feldmann, 2002 (fossil); *P. heckeri* (Birshtein, 1956) (fossil); *P. intermedia* (Collins & Morris, 1976, as *Thaumastoplax*) (fossil); *P. mytilicola* Vía Boada, 1966 (fossil); *P. perornata* Collins & Morris, 1976 (fossil); *P. prima* (Rathbun, 1918, as *Thaumastoplax*) (fossil); *P. rocaensis* (Feldmann, Casadio, Chirino-Gálvez & Aguirre-Urreta, 1995, as *Thaumastoplax*) (fossil); and *P. rotundus* Schweitzer & Feldmann, 2001 (fossil).

Parahexapus Balss, 1922 – includes only the type species *P. africanus* Balss, 1922 (extant).

Pseudohexapus Monod, 1956 – includes only the type species *P. platydactylus* Monod, 1956 (extant).

Spiroplax Mannin & Holtuis, 1981 – includes only the type species *S. spiralis* (Barnard, 1950, as *Thaumastoplax*) (extant).

Stevea Manning & Holthuis, 1981 – includes the type species *S. williamsi* (Glassell, 1938, as *Hexapus*) (extant); and “*Stevea*” *cesarii* Beschin, Busulini, De Angeli & Tessier, 1994 (fossil).

Thaumastoplax Miers, 1881 – includes only the type species *T. anomalipes* Miers, 1881 (extant).

Tritoplax Manning & Holtuis, 1981 – includes the type species *T. stebbingi* (Barnard, 1947, as *Hexapus*) (extant); and *T. stephensi* (Serène & Soh, 1976, as *Hexapus*) (extant).

Genus *Bellhexapus* nov.

Diagnosis: carapace only moderately wider than long; granular ornamentation on whole carapace and thoracic sternum; cervical and branchial grooves weakly distinct, only branchiocardiac groove marked by two deep branchiocardiac depressions; front very wide; orbits large, rounded; eyes kidney-shaped, not reduced; presence of a stridulatory apparatus, consisting of eight oblique, elongated, spaced striae, not situated on a prominent ridge; thoracic sternum very wide, markedly convex; sternites 5-7 approximately similar in size and shape; sutures 4/5, 5/6, 6/7 subparallel, nearly equidistant; presence of visible sternite 8 not ascertained; episternites 4-5 triangular, expanded posteriorly; male abdomen long, proportionally wide, strongly convex, surface smooth; most of somites free, separated by well distinct sutures; somite 1 not visible; somites 2-3 supposedly fused, without trace of sutures, showing as a long, wide, undivided, subrectangular plate; somite 6 the most developed, large, longer than wide, subrectangular, with a conspicuous lateral process, subproximally; absence of lateral sternal trenches in male.

Etymology: dedicated to Thomas Bell (1792-1880) for his studies on living and fossil decapods. Gender: masculine.

Type species: *Bellhexapus granulatus* n. sp., by present designation.

Description: as for the type species.

Discussion. *Bellhexapus* n. gen. has affinities with the extant *Spiroplax* Manning & Holthuis, 1981 (p. 176, fig. 37). Both genera share an oval, wider than long carapace, with antero-posteriorly convex lateral margins, wide front and orbits, and margins of the carapace with wide posterolateral indentations. However *Spiroplax* has a wider posterolateral indentation, a more enlarged male abdomen, and fused male abdominal somites 3-5 without visible sutures.

Bellhexapus n. gen. is easily recognised from the extant genera: *Paeduma* Rathbun, 1897, has a wider carapace, fused abdominal somites 3-5, a very long, narrow somite 6, with a strong constriction opposite to middle part of thoracic sternite 5, and a long telson. *Hexalaughlia* Guinot, 2006, has the male abdominal somites 3-5 fused, somite 6 as a relatively long, plate (Guinot, 2006).

Bellhexapus n. gen. may be distinguished from the other fossil hexapodid genera known to date, as follows:

Goniocypoda Woodward, 1867, differs in that its rectangular carapace is wider than long, the front is very narrow, the fronto-orbital width extends on

entire anterior margin of the carapace, the male abdominal somites are fused, either 3-5 or 5-6, and the sternite 4 has anterior projections (Schweitzer & Feldmann, 2001).

Hexapus De Haan, 1833, differs by: the carapace wider than long, enlarged posteriorly; branchiocardiac groove weakly developed, front straight, grooved medially, not extending beyond orbits, fronto-orbital margin wide about 32 percent of the maximum width of the carapace; male abdomen with somites 3-5 fused, lateral sternal trenches, either rather short and curved (*Hexapus sexpes*, Manning, 1982: fig. 1b) or extending almost to bases of mxp3 (*H. anfractus*, see Manning & Holthuis, 1981: fig. 33b; Manning, 1982).

Palaeopinnixa Vía Boada, 1966, differs in that the carapace is wider than long, rectangular, rounded or oval, and weakly restricted anteriorly, regions are marked, the front enlarges distally is grooved medially, and extends beyond orbits, the supraorbital margin is markedly sinuous, the posterolateral indentation is well developed, abdominal somites 3-5 are fused in the type species (Schweitzer *et al.*, 2000).

***Bellhexapus granulatus* n. sp.**

Figs. 2, 3

Diagnosis: as for the genus.

Etymology: the trivial name alludes to the ornamentation of the studied specimens.

Holotype: MCZ 3010-I.G.336840.

Paratype: MCZ 3011-I.G.336941.

Geological age: middle Eocene (middle Lutetian).

Type locality: "Albanello" quarry at Nogarole Vicentino (Vicenza).

Occurrence and measurements: two specimens. The holotype, a male (MCZ 3010-I.G.336840) with thoracic sternum and abdomen, and the paratype (MCZ 3011-I.G.336941) with carapace, chelipeds, and P2 merus.

MCZ 3010-I.G.336840: cl: 11.9; cw: 15.6; wo-f: 7.5; wf: 3.1

MCZ 3011-I.G.336941: cl: 14.1; cw: 18.6; wo-f: 8.5; wf: 3.2

Description: carapace moderately wider than long. Anterolateral margins slightly divergent posteriorly, markedly convergent anteriorly. Posterolateral margin straight, the external corner with a large notch corresponding to insertion of P4. Dorsal surface regularly covered by conspicuous granules, without indication of regions. Cervical and branchial grooves weakly distinct; branchiocardiac groove hardly visible, only two deep branchiocardiac depressions. Only a few other smaller pits, corresponding to muscle impressions. Gastric pits rounded, close to each other. Two blunt protogastric protuberances (Figs. 2A, 3C). Front broad, widening distally, markedly downturned, with slightly concave external borders; a faint median depression on frontal region. Orbits large, rounded, occupying the rest of the fronto-orbital margin. Supraorbital border rimmed (rim being granulous). Eye present, not reduced, showing as a curved structure, with short eyestalk and larger, kidney-shaped corneal area; conspicuous granules on superior border (Figs. 2B, 3E). Stridulatory apparatus consisting of oblique, elongated, well-spaced striae (no more than eight), not situated on a prominent ridge (Fig. 2B). Thoracic sternum markedly convex;

surface with same granular ornamentation as that of carapace. Sternite 4 much developed, inflated. Sternites 5-7 convex, approximately similar in size and shape. Sutures 4/5, 5/6, 6/7 subparallel, nearly equidistant. Presence of dorsally visible sternite 8 not ascertained (in any case very small). Episternites 4-5 triangular, much expanded posteriorly. Episternite 6 not triangular, small. Male abdomen long, proportionally wide, strongly convex, surface smooth. Several somites free, separated by distinct sutures. Somite 1 not visible. Somites 2-3 supposedly fused, without trace of sutures, showing as a long, wide, subrectangular plate, with convex lateral margins. Somites 4-5 wider. Somite 6 the most developed, large, longer than wide and subquadrate, with a conspicuous lateral process, subproximally; telson not preserved (Fig. 3B). Absence of lateral sternal trenches in male. Chelipeds robust, merus elongated, subcylindrical; carpus suboval, with rounded, granular surface; propodus as long as high; lower margin convex; upper margin short, curved; outer surface rounded, with many granules; fixed finger elongated, with a wide tooth on distal margin; movable finger elongated, curved, with two longitudinal granular ridges, one on outer surface, one on upper margin (Fig. 3D). P2 merus elongated, cylindrical, with granular upper margin (Fig. 3C).

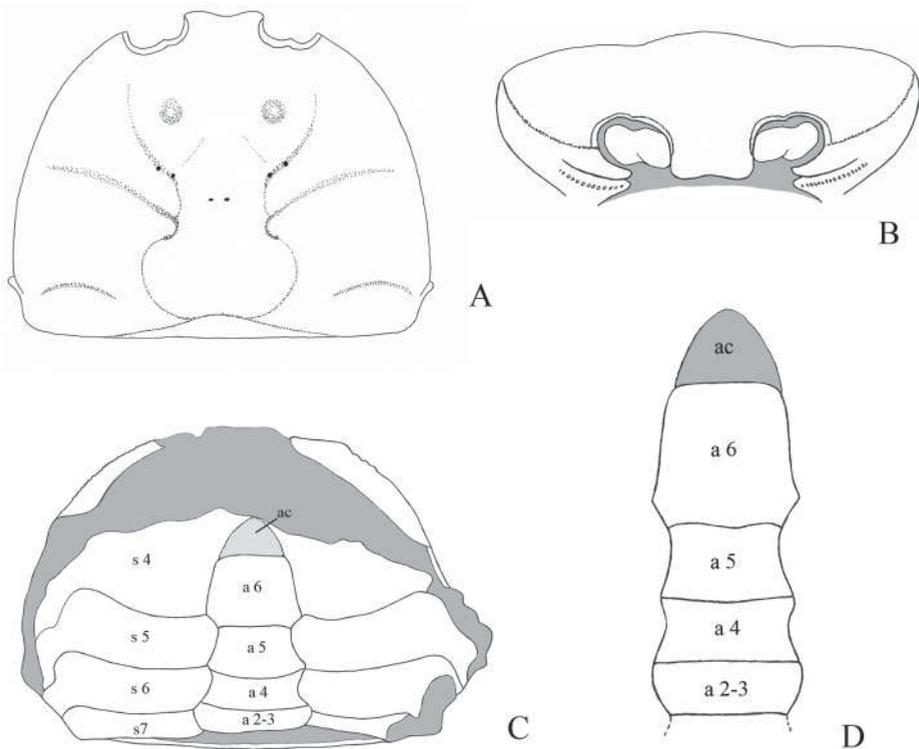


Fig. 2 - *Bellhexapus granulatus* n. gen., n. sp. A) reconstruction of carapace/ricostruzione del carapace. B) orbito-frontal view/visione orbito-frontale. C) ventral view/visione ventrale. D) male abdominal somites/somiti addominali maschili (s: sternite; a: abdominal somite/somite addominale; ac: sterno-abdominal cavity/cavità sterno-addominale).

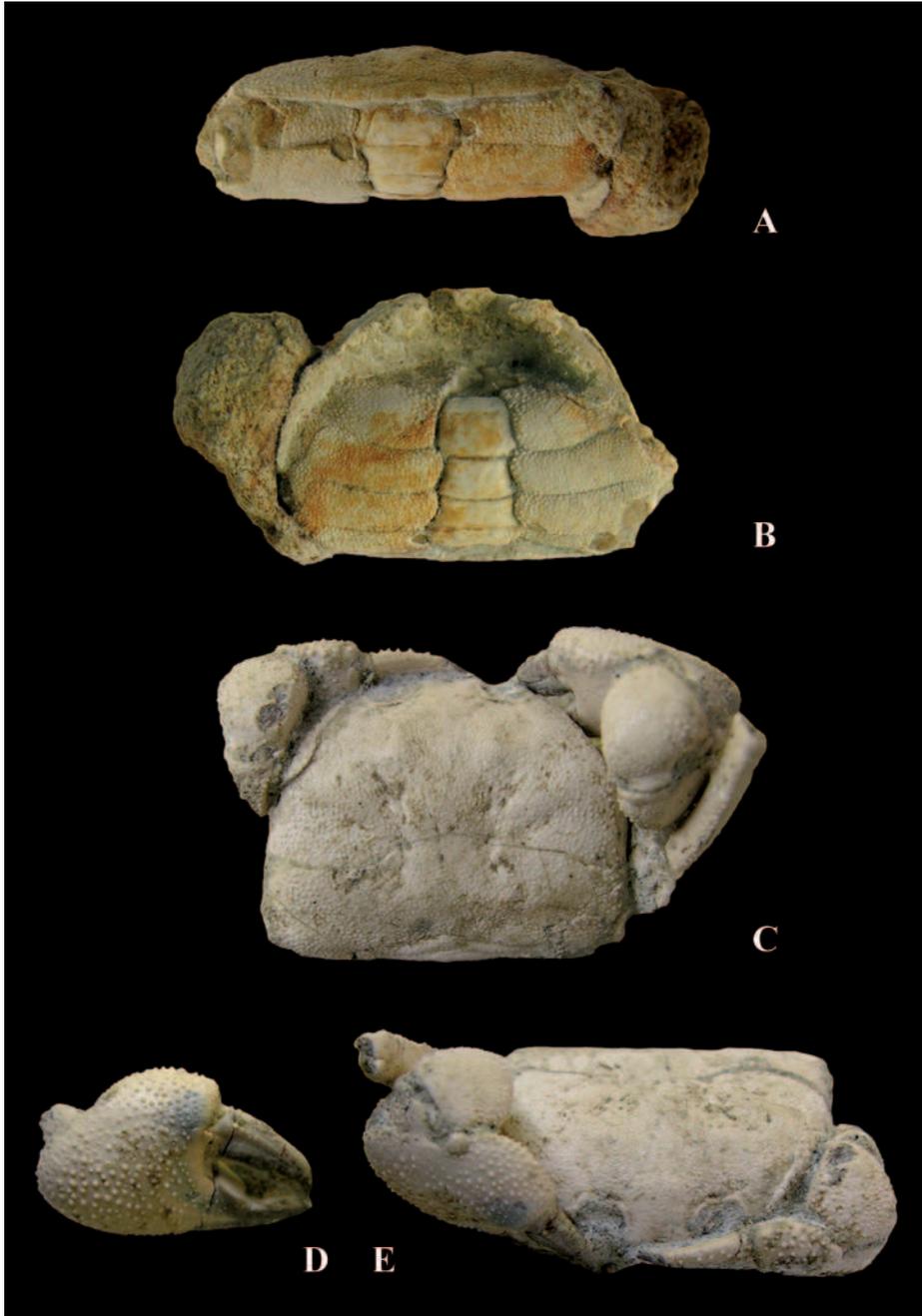


Fig. 3 - *Bellhexapus granulatus* n. gen., n. sp. A-B) holotype/olotipo MCZ 3010-I.G.336940 (x 3). A) posterior view/visione posteriore. B) ventral view/visione ventrale. C-E) paratype/paratipo, MCZ 3011-I.G.336941 (x 2.6). C) dorsal view/visione dorsale. D) right propodus/propodo destro. E) frontal view/visione frontale.

Discussion. *Bellhexapus granulatus* n. sp. is easily distinguished from “*Steeva*” *cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, discovered in “Albanello” quarry, by the different shape and ornamentation of carapace and by the different configuration of abdominal somites. In “*Steeva*” *cesarii* the carapace is suboval and wider than long, with a smooth dorsal surface, having only small pits (Beschin *et al.*, 1994: 192; Guinot *et al.*, in press).

Genus *Eohexapus* nov.

Diagnosis: carapace wider than long, subrectangular; wider anteriorly; lateral margin oblique, regularly converging anteriorly, reaching exorbital angle, with granulated ridge; dorsal surface convex longitudinally; cervical and branchiocardiac grooves absent; only two deep, rounded branchiocardiac depressions; front depressed, grooved medially; margin with obtuse angles and concave median part in frontal view; orbits as wide as high, with rounded supraorbital margin; thoracic sternum wide; sutures 4/5, 5/6, 6/7 equidistant; sternites 1-2 advanced between mxp3; sternite 3 well distinct demarcated by suture; sternite 4 well developed, with latero-anterior projections; sternites 5 to 7 inflated, about equal in size; sternite 8 not visible; male abdomen unknown; female abdomen relatively wide and long, with all free somites; somite 1 not visible; somite 2 subtrapezoidal; somites 3-4 rectangular, very wide; somites 5-6 progressively restricted anteriorly; somite 6 longer than somites 3-5, with convex margins; telson incomplete; sterno-abdominal cavity deep, extending on sternite 3, with convex margins; pterygostomial region granular; stridulatory apparatus consisting of a granular ridge.

Etymology: from Eocene, geological age, and *Hexapus*, type genus of the Hexapodidae. Gender: masculine.

Type species: *Eohexapus albertii* n. sp., by present designation.

Description: as for the type species.

Discussion. *Eohexapus* n. gen. has a carapace very enlarged anteriorly, in contrast to the other known hexapodids which show usually a more posteriorly enlarged carapace. This peculiarity allows only a comparison between the new genus and *Parahexapus* Balss, 1922, with only the type species *P. africanus* Balss, 1922, widespread along the sublittoral coast of West Africa (Ghana, Congo and Angola, from 5 to 22 metres) [Balss, 1922: 77, figs. 1-5; Monod, 1956: 370, figs. 494-496 as *Hexapus* (*Parahexapus*); Rossignol, 1962: 118 as *Hexapus* (*Parahexapus*); Crosnier, 1967: figs. 30, 33 as *Hexapus* (*Parahexapus*), Manning & Holthuis, 1981: 175, fig. 36a-c].

Eohexapus n. gen. and *Parahexapus* share the following characters: the subrectangular shape of the carapace, more enlarged anteriorly; the lateral margins obliques, converging posteriorly, with a granular ridge along the margin, the sternal region very enlarged, and the sterno-abdominal cavity deep, very elongated anteriorly. In *Parahexapus* sterno-abdominal cavity extends until the base of mxp3 (Balss, 1922: fig. 3), in *Eohexapus* n. gen. this cavity extends on all sternite 3 in the female (Figs. 4C, 5C). The carapace of *Parahexapus* has two depressed lines starting from the inner margin of the orbit and converging until the obsolete cervical groove; the cardiac region has some wide anterolateral and posterolateral depressions. The carapace of *Eohexapus* n. gen. has smooth dorsal surface,

without grooves, and the cardiac region with one wide anterolateral depression and one small posterolateral depression (Figs. 4A, 5A). The orbits of *Parahexapus* are small but extended dorsally on carapace; the front has projected lateral angles, and the frontal margin is slightly restricted at level of the orbits (Monod, 1956: 370, fig. 494). *Eohexapus* n. gen. differs by the orbits located transversally, not extending dorsally on carapace, and by the lateral angles of the frontal margin not extended laterally (Figs. 4B, 5B, 6A). In *Parahexapus* the telson of female is narrow and longer than wide (Balss, 1922: fig. 3; Monod, 1956: fig. 495); even though the telson of *Eohexapus* n. gen. is incomplete, it shows a more enlarged base than in *Parahexapus*. In *Parahexapus* the stridulatory apparatus is absent, while in *Eohexapus* n. gen. it shows as a granular ridge.

Eohexapus n. gen. is easily recognised from the others fossil genera known to date. *Goniocyopoda* Woodward, 1867, differs as follows: carapace subrectangular with rounded angles, front narrow, more enlarged distally, orbito-frontal width taking over all anterior margin of carapace, and orbits very wide, with sinuous supraorbital margin. *Palaeopinnixa* Vía Boada, 1966, differs as follows: carapace wider than long, more restricted in the anterior part, rounded along the margins, dorsal regions distinct, front enlarged distally, and orbits with sinuous supraorbital margins. *Hexapus* De Haan, 1833, differs as follows: carapace wider than long, more enlarged posteriorly, branchiocardiac groove weakly developed, lateral margins granular or with granular border, front straight, grooved medially, weakly projectecting beyond the orbits, orbits with sinuous, rimmed upper margin, and presence of lateral sternal trenches.

***Eohexapus albertii* n. sp.**

Figs. 4, 5, 6

Diagnosis: as for the genus.

Etymology: the trivial name alludes to Riccardo Alberti who discovered and cleaned the type specimen.

Holotype: MCZ 3004-I.G.336834.

Paratypes: MCZ 3005-I.G.336835, 3006-I.G.336836.

Geological age: middle Eocene (middle Lutetian).

Type locality: “Albanello” quarry at Nogarole Vicentino (Vicenza).

Occurrence and measurements: three specimens. The holotype, a female (MCZ 3004-I.G.336834) with thoracic sternum, abdomen, right cheliped, and some articles of the walking legs; MCZ 3005-I.G.336835 with the carapace and left cheliped; MCZ 3006-I.G.336836 with only the carapace.

MCZ 3004-I.G.336834: cl: 6.9; cw: 10.1; wo-f: 4.5; wf: 2.4

MCZ 3005-I.G.336835: cl: 9.1; cw: 13.3; wo-f: 5.6; wf: 2.7

MCZ 3006-I.G.336836: cl: 5.5; cw: 7.7

Description: carapace subrectangular, rounded along margins, convex antero-posteriorly, wider than long (cl/cw 0.68) with maximum width in median-anterior parts. Anterolateral margins rounded, marked by granular line; anterolateral margins converging posteriorly, forming oblique margin, ending to posterolateral angle by small rounded lobe. Posterior margin very wide (about 4/5 of maximum carapace width), slightly convex. Posterolateral indentation evident as a relatively wide concave relief. Orbito-frontal margin relatively wide (wo-f/cw 0.42).

Front depressed and grooved medially; distal part bilobate, with obtuse angles (Fig. 5B). Orbits small, rounded, as long as high, located transversally. Supra-orbital margin concave, not raised. Regions not defined. Dorsal surface mainly smooth, with numerous pits along lateral margins and frontal region. Two wide and rounded depressions on anterolateral portion of cardiac region; two other smaller depressions on posterolateral portion of cardiac region. Pterygostomial region granular. Stridulatory apparatus consisting of a granular ridge (Fig. 4C). Thoracic sternum very wide, finely punctate. Sutures 4/5, 5/6, 6/7 equidistant. Sternites 1-2 advanced between mpx3; sternite 1 short, obtuse-angled triangle in shape; sternite 2 with granular convex ridge; sternite 3 well distinct demarcated by suture; sternite 4 well developed, with latero-anterior projections; sternites 5 to 7 inflated, about equal in size; sternite 7 tilted; episternite 7 with rounded posterolateral corner; sternite 8 not visible. Female abdomen relatively wide, long, with all free somites; somite 1 not visible; somite 2 covered by somite 3, but visible in posterior view; somites 3-4 rectangular, very wide; somites 5-6 progressively restricting anteriorly; sternite 6 longer than somites 3-5, with concave margin; telson incomplete, preserving only the base. Sterno-abdominal cavity deep, extending on sternite 3. Cheliped palm as high as long, with rounded, tuberculated outer surface. Absence of lateral sternal trenches.

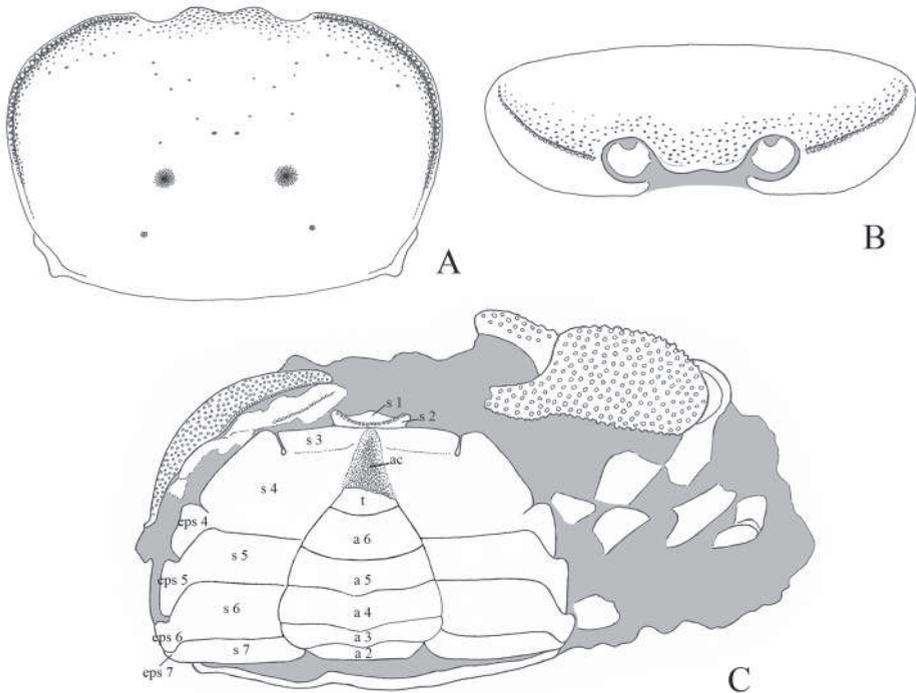


Fig. 4 - *Eohexapus albertii* n. gen., n. sp. A) reconstruction of carapace/ricostruzione del carapace. B) orbito-frontal view/visione orbito-frontale. C) ventral view/visione ventrale (s: sternite; eps: episternite; a: abdominal somite/somite addominale; t: telson; ac: sterno-abdominal cavity/cavità sterno-addominale) (from holotype/da olotipo).

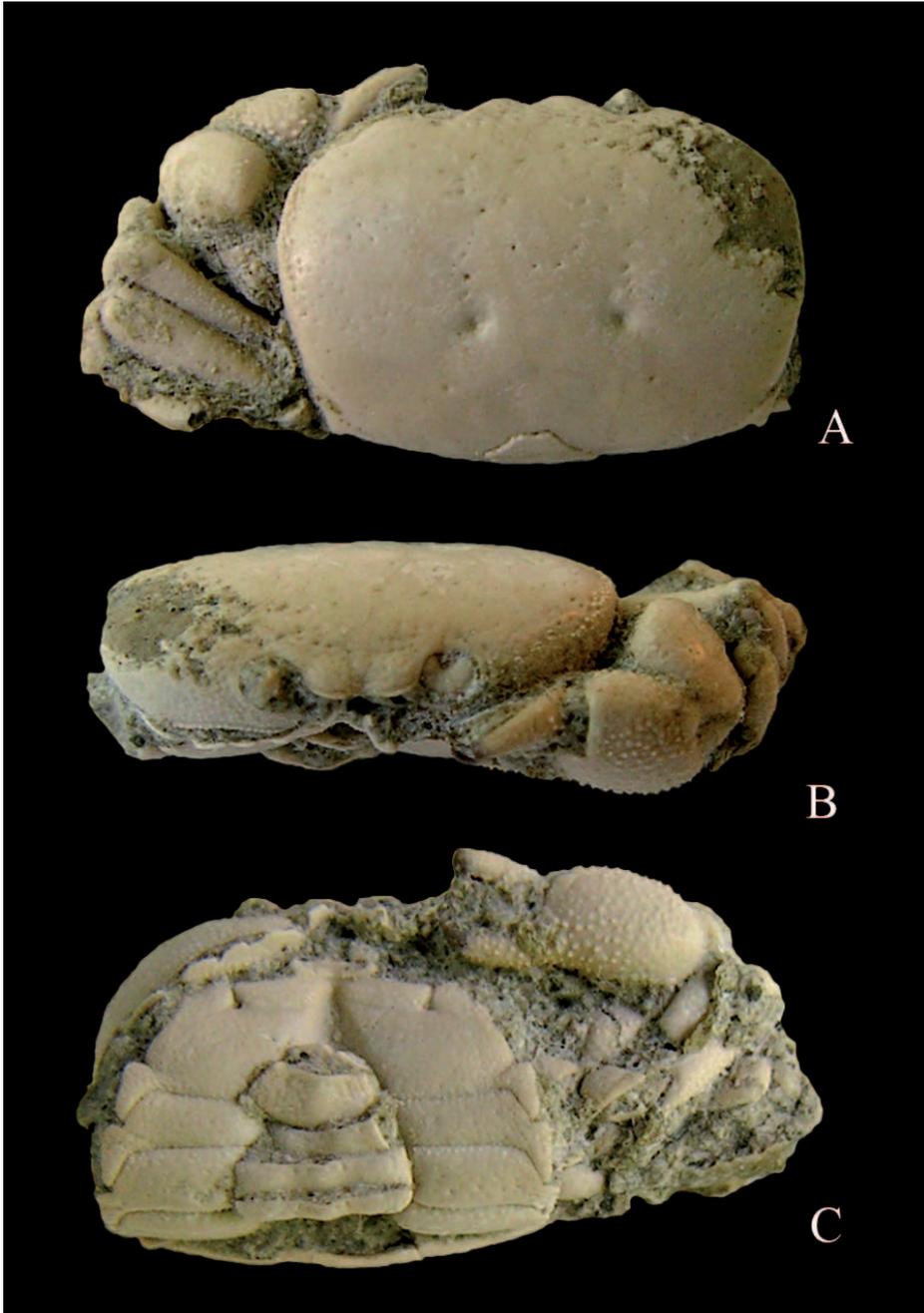


Fig. 5 - *Eohexapus albertii* n. gen., n. sp. Holotype/olotipo MCZ 3004-I.G.336834 (x 6.5). A) dorsal view/visione dorsale. B) frontal view/visione frontale. C) ventral view/visione ventrale.

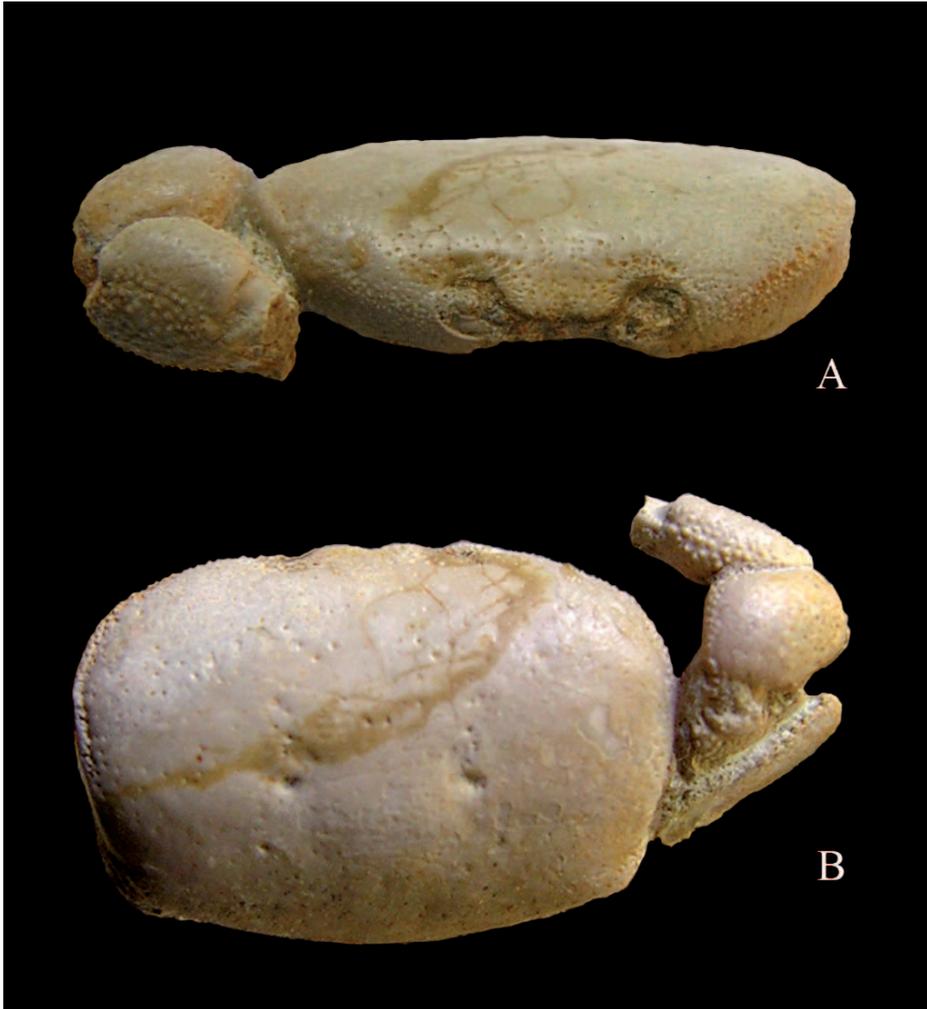


Fig. 6 - *Eohexapus albertii* n. gen., n. sp. Paratype/paratipo MCZ 3005-I.G.336835 (x 5.6). A) frontal view/visione frontale. B) dorsal view/visione dorsale.

Discussion. *Eohexapus albertii* n. gen., n. sp. is quite distinct from “*Stevea*” *cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, and from *Bellhexapus granulatus* n. gen., n. sp. “*Stevea*” *cesarii* differs in that the suboval carapace is more enlarged posteriorly, with convex lateral margins, the front is depressed and grooved medially, the orbits are elongated, with rounded and rimmed supraorbital margin (Guinot *et al.*, in press). In *Bellhexapus granulatus* n. gen., n. sp. the carapace is wider than long, with convex lateral margins, and the granular dorsal surface has only two deep branchiocardiac depressions.

Genus *Eurohexapus* nov.

Diagnosis: carapace subquadrate; dorsal surface undulated, with regions defined by protuberances, in particular a large, inflated cardiac region; grooves indistinct, at the exception of deep, short branchiocardiac groove delimiting salient internal epibranchial lobe; presence of several conspicuous depressions in gastric region; orbits enormous; front very wide, long, strongly downturned, tapering distally; thoracic sternum very wide, convex; sternites 5-7 approximately similar in size and shape; sternite 8 not visible; episternites 4-6 elongated, pointed; sutures 4/5, 5/6, 6/7 nearly parallel, equidistant; male abdomen with fused somites 2-6, but with all sutures distinct, notably by median fissure; somite 6 with subproximal lateral process; presence of three ventral protuberances, one on abdominal somite 6 and on each side of sternite 4; absence of lateral sternal trenches in male; stridulatory apparatus not observable.

Etymology: from “Europe” and *Hexapus*, type genus of the Hexapodidae. Gender: masculine.

Type species: *Eurohexapus lobatus* n. sp., by present designation.

Description: as for the type species.

Discussion. *Eurohexapus* n. gen. markedly differs from all other hexapodids. The genus is characterized by the relatively narrow, subquadrate carapace, and by the almost parallel, moderately convex lateral margins (Figs. 7A, 8A, 9A). The carapace of most hexapodids is subrectangular or rounded-rectangular, and more enlarged posteriorly. The dorsal surface has the regions well marked by protuberances and presence of several conspicuous depressions in the gastric region, corresponding in particular to the insertion of the attractor epimeralis muscle (Glaessner 1969: R408, fig. 224; Renaud, 1977: fig. 1). Among the known hexapodids, only *Latohexapus* Huang, Hsueh & Ng, 2002, has the dorsal carapace regions which are clearly demarcated, separated by deep grooves and ornamented with tubercles; however its carapace is much wider than long and more enlarged posteriorly. Other characteristics of *Eurohexapus* are as follows: fronto-orbital margin very wide ($w_o-f/cw = 0.60$), front strongly depressed, grooved medially; and, in frontal view, long and restricted distally (Figs. 7B, 8B). The well preserved ventral parts of the holotype, show three ventral protuberances, two on the sternite 4 and one on abdominal somite 6 (Figs. 7C, 8E).

Eurohexapus n. gen. has fused male abdominal somites 2-6, with all sutures that are still distinct, notably by a median fissure (Figs. 7D, 8E-F). Among the known hexapodids, *Stevea* Manning & Holthuis, 1981, shares the same characters, but in *Stevea* only small lateral sutures are present and the abdominal somite 6 is very elongate (Guinot, 2006: fig. 3 B, C; Guinot *et al.*, in press).

Eurohexapus lobatus n. sp.

Figs. 7, 8, 9

Diagnosis: as for the genus.

Etymology: *lobatus -a -um* (lat.), referring to the well-defined surface of the carapace.

Holotype: MCZ 3007-I.G.336837.

Paratypes: MCZ 3008-I.G.336838, 3009-I.G.336839.

Geological age: middle Eocene (middle Lutetian).

Type locality: “Albanello” quarry at Nogarole Vicentino (Vicenza).

Occurrence and measurements: three specimens. The holotype, a male (MCZ 3007-I.G.336837), with left cheliped, thoracic sternum, and abdomen; MCZ 3008-I.G.336838 with incomplete carapace, chelipeds, and fragments of walking legs (three legs); MCZ 3009-I.G.336839 with carapace and chelipeds.

MCZ 3007-I.G.336837: cl: 12.5; cw: 12.5; wo-f: 7.5; wf: 3

MCZ 3008-I.G.336838: not measurable.

MCZ 3009-I.G.336839: cl: 12.5; cw: 12.5; wo-f: 7.5; wf: 3.1

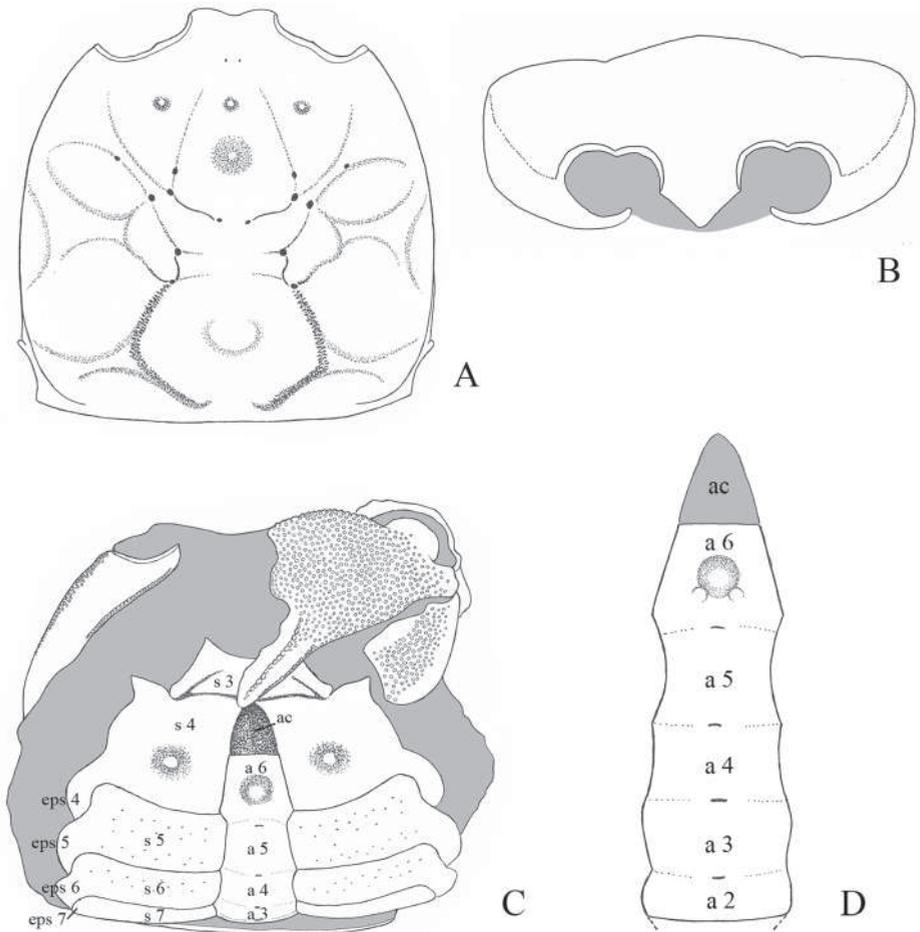


Fig. 7 - *Eurohexapus lobatus* n. gen., n. sp. A) reconstruction of carapace/ricostruzione del carapace. B) orbito-frontal view/visione orbito-frontale. C) ventral view/visione ventrale. D) male abdominal somites/somiti addominali maschili (s: sternite; eps: episternite; a: abdominal somite/somite addominale; ac: sterno-abdominal cavity/cavità sterno-addominale).

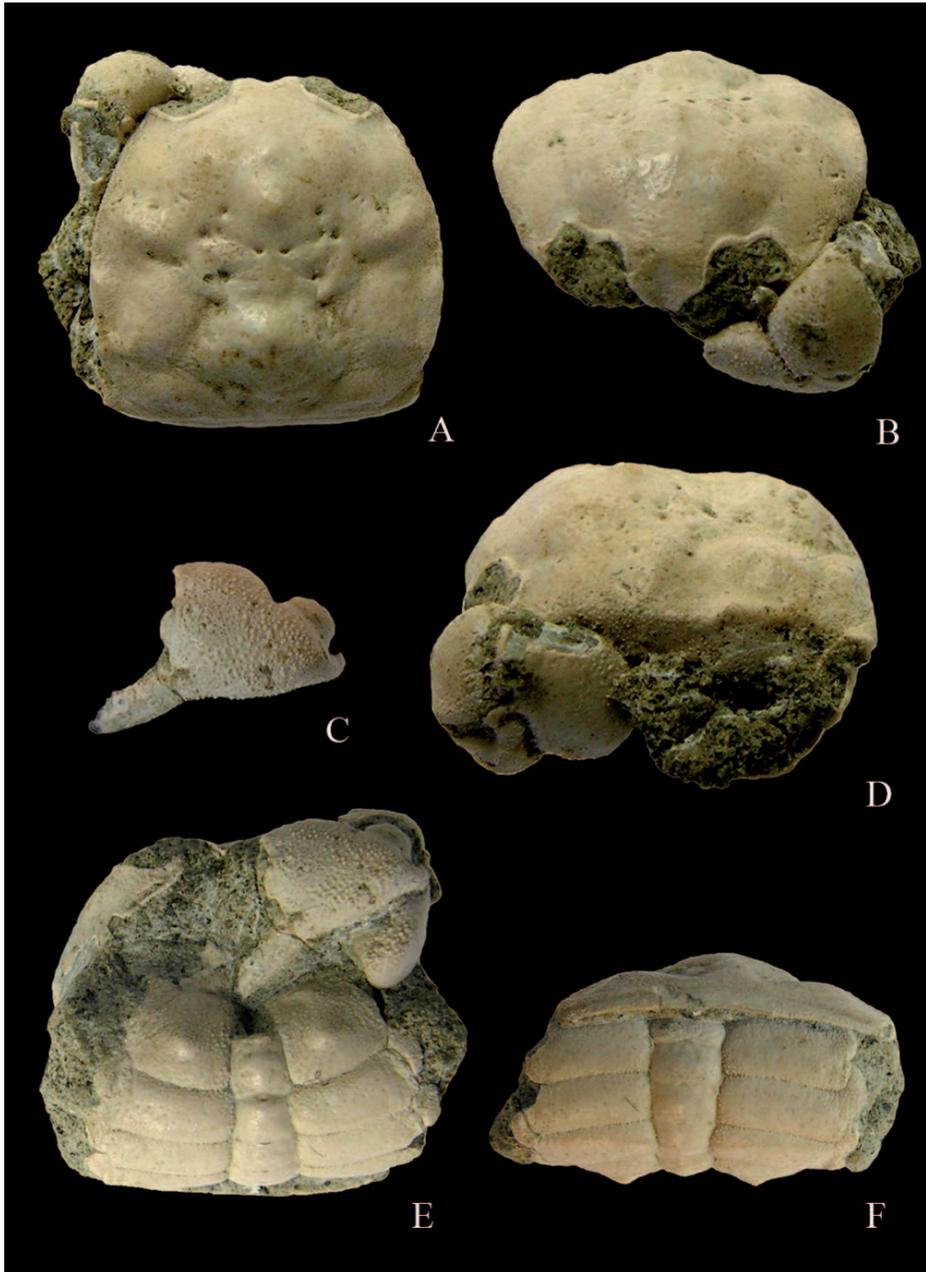


Fig. 8 - *Eurohexapus lobatus* n. gen., n. sp. Holotype/olotipo MCZ 3007-I.G.336837 (x 3.7). A) dorsal view/visione dorsale. B) frontal view/visione frontale. C) left propodus/propodo sinistro. D) lateral view/visione laterale. E) ventral view/visione ventrale. F) posterior view/visione posteriore.

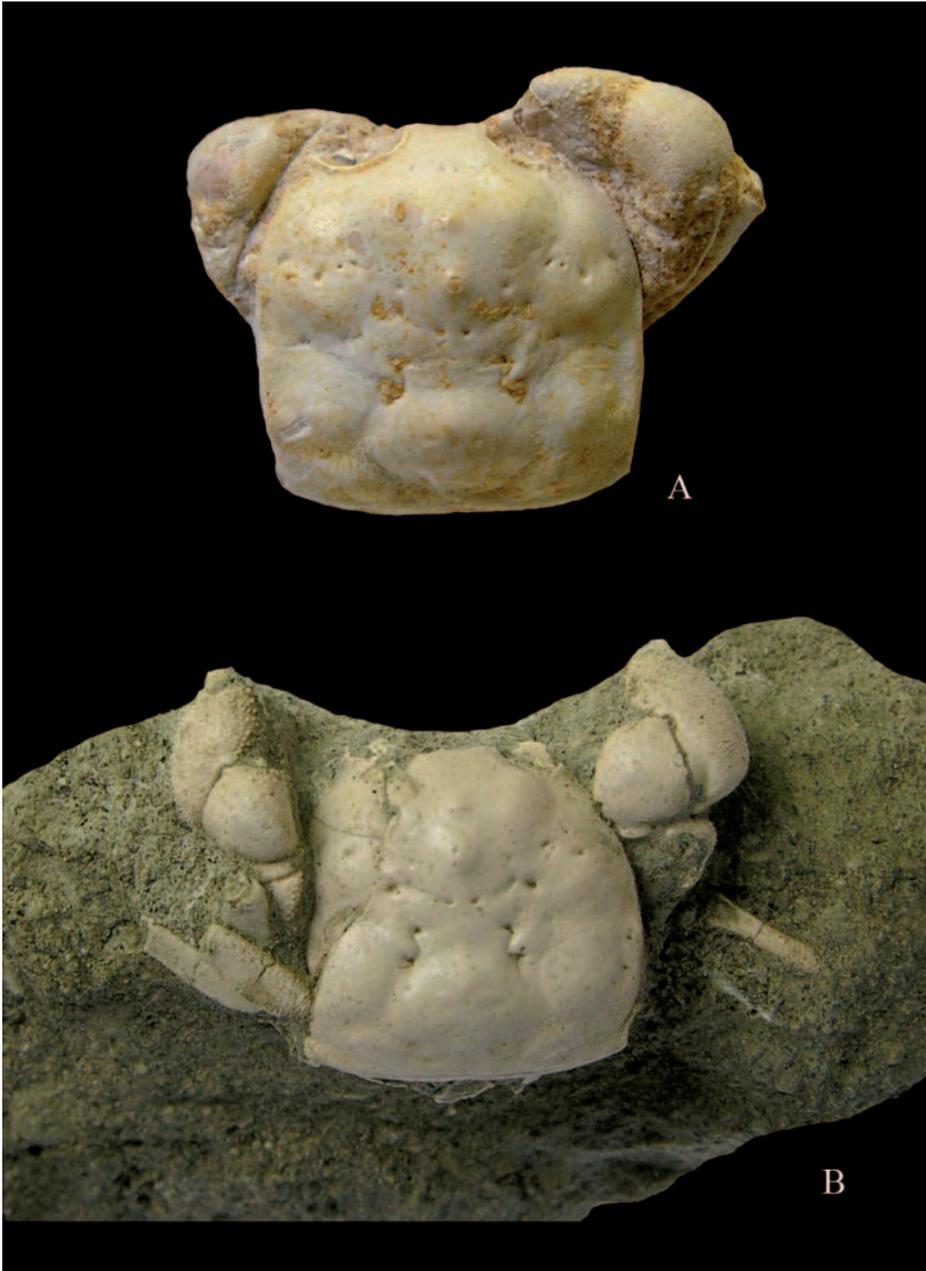


Fig. 9 - *Eurohexapus lobatus* n. gen., n. sp. A) paratype/paratipo MCZ 3009-I.G.336839, dorsal view/visione dorsale (x 4). B) paratype/paratipo MCZ 3008-I.G.336838, dorsal view/visione dorsale (x 3.9).

Description: carapace only slightly longer than wide, subquadrate. Lateral margins subparallel for most length, convergent anteriorly. Posterolateral margin straight, distinctly rimmed, with a large notch at the external corner, corresponding to insertion of P4. Dorsal surface undulated, with indication of some regions. Grooves indistinct, at the exception of deep, short branchiocardiac groove delimiting well marked internal epibranchial lobe. Cardiac region large, subhexagonal, well delimited and very inflated. Two elevated mesogastric protuberances; external epibranchial, mesobranchial and metabranchial regions defined by protuberances. Gastric pits deep, nearly horizontal, close to each other. Numerous conspicuous depressions distributed on gastric region, corresponding to muscle attachment (Figs. 7A, 8A, 9A-B). Orbits enormous; supraorbital margin thick, sinuous, strongly rimmed; front very wide, long, strongly downturned, axially sulcate, with distally subparallel margins then proximally converging margins (Figs. 7B, 8B). Thoracic sternum convex; sternite 3 partially visible; sternite 4 much developed, inflated, with distinct lateroanterior projection and submedian prominence on each side; surface granulous; sternites 5-7 convex, subequal in size, with granules lining abdominal border; sutures 4/5, 5/6, 6/7 subparallel, nearly equidistant, lined by granules; sternite 8 not visible, even partially; episternites 4-6 triangular, much developed, each overlapping large portion of following sternite; episternite 7 not triangular, with convex border. Male abdomen rather long and wide; somite 1 not visible; somites 2-6 fused, with sutures still distinct, notably by median fissure; telson not preserved; somite 2 short; somites 3-5 longer; somite 6 most developed, with lateral process, subproximally with median prominence slightly smaller than those on each side of sternite 4 (Figs. 7C, 8E-F). Absence of lateral sternal trenches in male. Chelipeds strong, merus elongated, subcylindrical, with granular lower and upper margins; carpus suboval, with rounded, granular surface; palm as long as high, with elongated, convex lower margin, and short, curved upper margin; outer surface curved, with granulation; fixed finger elongated, with granular ridge on outer margin (Fig. 8C). Meri of walking legs equal in size, with small granulations (Fig. 9B).

Discussion. *Eurohexapus lobatus* n. gen., n. sp. differs from “*Stevea*” *cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, *Bellhexapus granulatus* n. gen., n. sp., and *Eohexapus albertii* n. gen., n. sp., collected in the same “Albanello” quarry, by the shape and ornamentation of the carapace, front-orbital margin, and different disposition of abdominal somites.

Genus *Palaeopinnixa* Vía Boada, 1966

Type species: *P. rathbunae* Schweitzer, Feldmann, Tucker & Berglund, 2000 (= *Pinnixa eocenica* Rathbun, 1926, by original designation)

Palaeopinnixa alontensis n. sp.

Figs. 10, 11

2009 - *Palaeopinnixa* sp. in Busulini & Beschin; p. 116, figs. 9, 10

Diagnosis: carapace rounded-rectangular, wider than long, more enlarged posteriorly, convex in longitudinal section; front wider distally, grooved medially; orbits

small, suboval; orbital margin sinuous; regions moderately developed; branchio-cardiac groove deep; dorsal surface smooth, with two small pits between hepatic and branchial regions.

Etymology: the trivial name alludes to Alonte, where the studied specimens were discovered.

Holotype: MCZ 3002-I.G.336832.

Paratypes: MCZ 3003-I.G.336833, MSNM i27405, i27406, i27407, i27408, i27409, i27410.

Stratigraphic range: upper Eocene (Priabonian).

Type locality: Alonte (Monti Berici, Vicenza).

Occurrence and measurements: eight carapaces (MCZ 3002-I.G.336832, 3003-I.G.336833, MSNM i27405, i27406, i27407, i27408, i27409, i27410).

MCZ 3002-I.G.336832: cl: 14.2; cw: 21.7; wo-f: 7.0

MCZ 3003-I.G.336833: cl: 15.7; cw: 24.6; wo-f: 8.2

MSNM i27405: cl: 14.2; cw: 22.1; wo-f: 7.2; wf: 3.3

MSNM i27406: cl: 5.6; cw: 8.5

MSNM i27407: cl: 14.7; cw: 25; wo-f: 8.3

MSNM i27408: cl: 13.6; cw: 20.5

MSNM i27409: cl: 8.9; cw: 12.3

MSNM i27410: cl: 17.7; cw: 26.4; wo-f: 8.8

Description. Carapace convex longitudinally, rounded-rectangular in outline, wider than long (cl/cw about 0.64), more enlarged posteriorly. Dorsal surface mainly smooth, with two conspicuous oval depressions distributed on hepatic and branchial regions, corresponding to muscle attachments. Branchiocardiac groove deep, well distinct only on anterior part of cardiac region; branchiocardiac groove connected with a weak groove until outer margin of orbit, delimiting externally gastric regions; metagastric and urogastric regions marked by weak posterior groove. Gastric pits rounded, close to one another; cardiac region weakly raised, faintly delimited from intestinal and branchial regions. Fronto-orbital margin weakly wide (wo-f/cw about 0.33); frontal margin about 15 percent maximum carapace width; front depressed, grooved medially, wider distally, extending beyond orbits. Orbits wider than long;

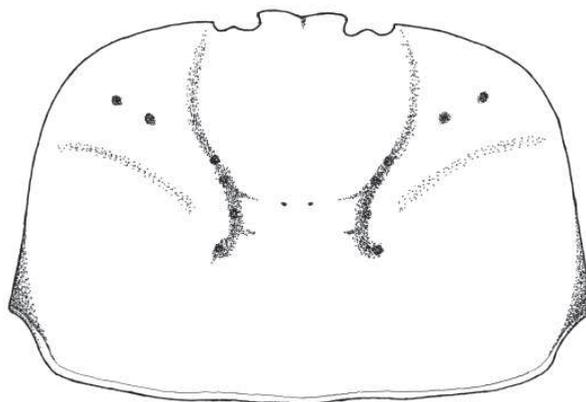


Fig. 10 - *Palaeopinnixa alontensis* n. sp., reconstruction of carapace/ricostruzione del carapace.



Fig. 11 - *Palaeopinnixa alontensis* n. sp. A-B) holotype/olotipo MCZ 3002-I.G.336832 (x 3.3). A) dorsal view/visione dorsale. B) frontal view/visione frontale. C-D) paratype/paratipo MCZ 3003-I.G.336833 (x 2.5). C) dorsal view/visione dorsale. D) frontal view/visione frontale.

supraorbital margin sinuous. Anterolateral margin convex, divergent until posterolateral indentation, point of maximum width; posterolateral indentation well developed. Posterior margin very wide, almost straight. Ventral parts not preserved.

Discussion. Schweitzer *et al.* (2000) raise *Palaeopinnixa* Vía Boada, 1966, to full generic status, and moved it from the Pinnotheridae to the Hexapodidae, including in this genus some species previously ascribed to *Thaumastoplax*. Later Schweitzer & Feldmann (2001) discussed the characters of *Palaeopinnixa* and gave a check list of all included species.

The studied specimens have the carapace similar to that of some known fossil species of *Palaeopinnixa*; in particular the rounded-rectangular carapace, more restricted anteriorly, with distinct regions, and well developed posterolateral indentation. However, *P. alontensis* n. sp. differs from the other fossil species, as follows: *P. granulosa* Schweitzer & Feldmann, 2002 (Eocene - United States) has a wider carapace, with granular surface; *P. intermedia* (Collins & Morris, 1976) (middle Miocene - Trinidad) has a rectangular carapace; *P. perornata* Collins & Morris, 1976 (early or middle Eocene - Barbados), *P. prima* (Rathbun, 1918) (Oligocene - Panama), *P. rocaensis* (Feldmann, Casadio, Chirino-Gálvez & Aguirre-Urreta, 1995) (late Eocene - United States), *P. rathbunae* Schweitzer, Feldmann, Tucker & Berglund, 2000 (Eocene - United States), and *P. rotundus* Schweitzer & Feldmann, 2001 (middle-late Eocene - United States) have a well marked cardiac region, with three tubercles; *P. mytilicola* Vía Boada, 1966 (Miocene - Spain) has a wider fronto-orbital margin and the cardiac region well marked by grooves.

The carapace of *P. alontensis* n. sp. shows two wide rounded depressions between the hepatic and branchial regions; the cardiac region well marked only anteriorly, with its posterior parts smooth and not marked by groove (Figs. 11 A, C).

Palaeopinnixa sp. from the upper Eocene of Possagno (Treviso), described by one inner cast (Busulini & Beschin, 2009: 116, figs. 9, 10) is identical to *P. alontensis* n. sp. by having the same diagnostic character.

Conclusion

The living Hexapodidae is known to be highly modified for symbiosis in polychaete tubes and the body cavities of hydrozoans (Manning & Holthuis, 1981; Pereyra Lago, 1988: 587). Tesch (1918: 238) commented that their commensalistic mode of life “has brought about not only the cylindrical shape of the body, but also the disappearance of the posterior legs, which, by the fact that they are inserted at a higher level than the preceding pairs, perhaps would rather impair the animal’s moving up and down in the tubes of Annelids and Hydrozoa”. Gordon (1971: 106) explained the loss of the last leg as a result of the lack of room for the P5 when the carapace and sternum are interlocked. In addition to body shape, the reduction of sternite 8 and (apparent) loss of the last leg were interpreted by all authors as the result of hexapodid life style. It should be noted that, the P5 is not completely aborted, a vestigial coxa being articulated to the reduced sternite 8 in much part (Guinot, 2006; Guinot *et al.*, in prep.). Hexapodidae are clearly true decapods, having five pairs of legs, with P5 strongly reduced.

The long accepted assertion that the transversally elongated carapace and absence of marked ornamentation allow hexapodids to move inside restricted tubular spaces, animal tubes, and body cavities, in particular in annelids (Zehntner, 1894; Gordon, 1971), well applies for a number of species. But other hexapodids as *Latohexapus granosus* Huang, Hsueh & Ng, 2002, with a wide, heavily ornamented body are so far known free living in soft bottoms. *Tritoplax* sp. in Stephensen, 1946 (p. 182, fig. 53B, as *Hexapus sexpes*, Manning & Holthuis, 1981: 180), with a wide, smooth carapace, is recorded from clay bottom in the Iranian Gulf (Stephensen, 1946: 185). A few others, such as *Spiroplax spiralis* which lives in intertidal sandy muddy sediment inhabited by thalassinoids (Pereyra Lago, 1988: 576) lack a transversally elongated carapace.

Eurohexapus lobatus n. gen., n. sp., is a true hexapodid as shown by its typical thoracic sternum but it is characterized by a subquadrate longer carapace; therefore it is unusual for an hexapodid; its sternite 8 is not dorsally visible, being completely covered by the carapace. Its possible symbiosis inside restricted tubular spaces is questioned. *Bellhexapus granulatus* n. gen., n. sp., also shows a rather subquadrate carapace, with coarsely tuberculated regions. *Eurohexapus* n. gen. and *Bellhexapus* n. gen. have a narrow and convex carapace and, nevertheless, their thoracic sternum is very wide, the sternite 8 is reduced and overlapped by the carapace, and the P5 is evidently absent (for most part at least). These two hexapodids have not probably adapted their body for symbiosis with polychaete tubes and body cavities of hydrozoans. Further investigations are needed to understand the origin of the unique organization of the Hexapodidae.

Bellhexapus granulatus n. gen., n. sp., *Eohexapus albertii* n. gen., n. sp., *Eurohexapus lobatus* n. gen., n. sp., and “*Stevea*” *cesarii* come from the same “Albanello” quarry at Nogarole Vicentino. The fossiliferous level (volcanodetritic marls) is rich in foraminiferans, nummulites, echinoids, and molluscs, belonging to the rich fauna of “Orizzonte di San Giovanni Ilarione” (Mellini & Quaggiotto, 1988). Polychaete tubes are not reported for this level. One stomatopod, one palinurid, and many brachyurans are known from the same quarry (De Angeli & Garassino, 2006).

The Hexapodidae, known by a scarce number of extant, fossil genera and species, is represented in the same quarry by four species, living in the same environment. The specimens of “*Stevea*” *cesarii* are frequent in the quarry, while those of *Bellhexapus granulatus* n. gen., n. sp., *Eohexapus albertii* n. gen., n. sp., and *Eurohexapus lobatus* n. gen., n. sp. are scarce.

The volcanodetritic marls of “Albanello” quarry were deposited in a warm, shallow environments (Beschin *et al.*, 2001). The quick sedimentation without strong alteration has preserved the most part of the fossils of this quarry. In fact some decapods were discovered complete, also with preserved ventral parts and pereopods: for instance the palinurid *Justitia vicentina* Beschin, De Angeli & Garassino, 2001, has preserved the abdominal parts, pereopods, and fragments of the antennae; some retroplumids, such as *Retrocypoda almelai* Via Boada, 1959, and *Retropluma eocenica* Via Boada, 1959, have preserved the ventral parts and chelipeds (Beschin *et al.*, 1996, 2001).

Palaeopinnixa alontensis n. sp. was instead discovered in a well stratified calcarenites, rich in casts of molluscs and corals. This species lived associated with other decapod crustaceans, such as *Italialbunea lutetiana* (Beschin &

De Angeli, 1984), *Priabonella violatii* Beschin, De Angeli, Checchi & Mietto, 2006, *Eopalicus imbricatus* De Angeli & Beschin, 2000, and *Spinipalicus italicus* Beschin & De Angeli, 2003.

The discovery of three new genera and four new species of fossil hexapodids confirms the extraordinary wealth of decapod crustaceans living during the Eocene in the Tethys Sea of northeastern Italy. The presence of four different species cohabiting the same environment of the Eocene layers of “Albanello” quarry represents an unusual fact, since the known fossil record of the Hexapodidae is rare and usually located in few deposits.

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