



The first record of a paguroid shield (Decapoda, Anomura, Annuntidiogenidae) from the Miocene of Cyprus

Prva najdba ščitov rakov samotarjev (Decapoda, Anomura, Annuntidiogenidae) iz miocenskih plasti Cipra

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Abstract

For the first time, a paguroid shield is recorded from upper Miocene reefal strata (Koronia Member, Pakhna Formation) that crop out along the northern margin of the Troodos Massif, north of the village of Mitsero, Cyprus. Described here as *Paguristes joecollinsi* sp. nov., it constitutes the first paguroid shield known from Miocene deposits. The paucity of Cenozoic paguroid shields can probably be linked to a collecting bias in view of their relatively small size; in addition, suitable gastropod shells and internal moulds of such should be screened for 'hidden' hermit crabs.

Izvleček

Predstavljamo prvo najdbo ščita raka samotarja iz zgornjemiocenskih grebenskih apnencev (člen Koronija, formacija Pakhna), ki izdanjajo vzdolž severnega roba masiva Troodos, severno od vasi Mitsero na Cipru. V prispevku predstavljamo novo vrsto *Paguristes joecollinsi* sp. nov., ki je hkrati tudi prva najdba paguroidnega ščita miocenske starosti. Odsotnost kenozojskih paguroidnih ščitov je verjetno povezana z njihovo majhnostjo, saj jih hitro spregledamo. Pri iskanju ostankov rakov samotarjev je treba natančno preveriti tudi lupine in kamena jedra polžev.

Introduction

Up to now, abundant paguroid shield material has been recorded only from Jurassic reefal deposits (e.g., Van Bakel et al., 2008; Fraaije, 2014a; Fraaije et al., 2019) and mid- and Upper Cretaceous strata of comparable lithologies (e.g., Fraaije et al., 2008, 2009, 2012). In stark contrast is the current record of just a single hermit crab shield from Eocene coral-algal limestones in northern Italy as recorded by Beschin et al. (2016, 2017) and of an individual of *Dardanus colosseus*, preserved *in situ* in an internal mould of a gastropod from the Eocene of Austria (Fraaije

& Polkowsky, 2016). Recently, six partially preserved shields have been briefly described and illustrated on the internet by a private collector, who had recovered them from reefal strata of Danian age at a quarry near Vigny (Paris Basin, France) (Buridan.over-blog.com 2018). All of the above constitute the current meagre record of paguroid shields of Paleogene and Neogene age that we are aware of.

Although relatively common in the fossil record, hermit crabs rarely become fossilised within the empty gastropod shells they usually inhabit.

Miocene	Messinian	Kalavastos Fm	
	Tortonian	Pakhna Fm	★ Koronia Lst
	Serravallian		
	Langhian		
	Burdigalian		
	Aquitanian		Terra Lst

Fig. 1. Stratigraphical position (asterisk) of the holotype and sole specimen of *Paguristes joecollinsi* sp. nov. known to date.

it, probably because the animals abandon these when under stress (Dunbar & Nyborg, 2003). Alternative hypotheses are that the hard parts fall out of the gastropod shell upon decay of the hermit crab and not all Mesozoic hermit crabs inhabited gastropods (e.g., Fraaije, 2003). A recent study by Klompmaker et al. (2017) has revealed that the decay of complete paguroid animals is a rapid process, in comparison to other decapod crustaceans such as lobsters and crabs. They also demonstrated that, in addition to paguroid claws, anterior carapaces (shields) also have a relatively high preservational potential compared to the less calcified posterior shield. This result suggests that the paucity of extinct paguroid carapaces/shields might be a matter having been overlooked by collectors in the field on account of their small to diminutive size in comparison to other associated decapod crustaceans. Additionally, extensive checking of the content of gastropod shells or their internal moulds is likely to yield more paguroid specimens.

The new specimen described here was collected in May 2017 by one of us (RHBF) while doing fieldwork together with the fourth author (AAK) in upper Miocene reefal deposits at Mitsero, Cyprus (Figs. 1, 2). Following the record of a new, shallow-water munidopsid anomuran by Fraaije (2014b), this is only the second study on decapod crustaceans from the Miocene of Cyprus. More material from various localities in Cyprus is now contained in the collections of the Oertijdmuseum at Boxtel (the Netherlands). Below we adopt the morphological terminology of paguroid carapaces as described by Fraaije et al. (2019).

Institutional abbreviation: MAB, Oertijdmuseum, Boxtel, the Netherlands.

Systematic palaeontology

Order Decapoda Latreille, 1802

Infraorder Anomura MacLeay, 1838

Superfamily Paguroidea Latreille, 1802

Family Annuntidiogenidae Fraaije, 2014a

Genus *Paguristes* Dana, 1851

Type species: *Paguristes hirtus* Dana, 1851, by the subsequent designation of Stimpson (1858).

Included species: For fossil taxa, reference is made to Gagnaison (2012), Fraaije et al. (2015, table 1), Karasawa & Fudouji (2018, p. 23) and Beschin et al. (2018). For extant species, see Lemaitre & McLaughlin (2019).



Fig. 2. Location of a number of basins with Miocene strata, with the type locality of *Paguristes joecollinsi* sp. nov. marked by a large asterisk; the provenance of the only other anomuran recorded to date from the Miocene of Cyprus, *Palmunidopsis muelleri* Fraaije, 2014b, is marked by a small asterisk. Image modified from Fraaije (2014b, fig. 1)

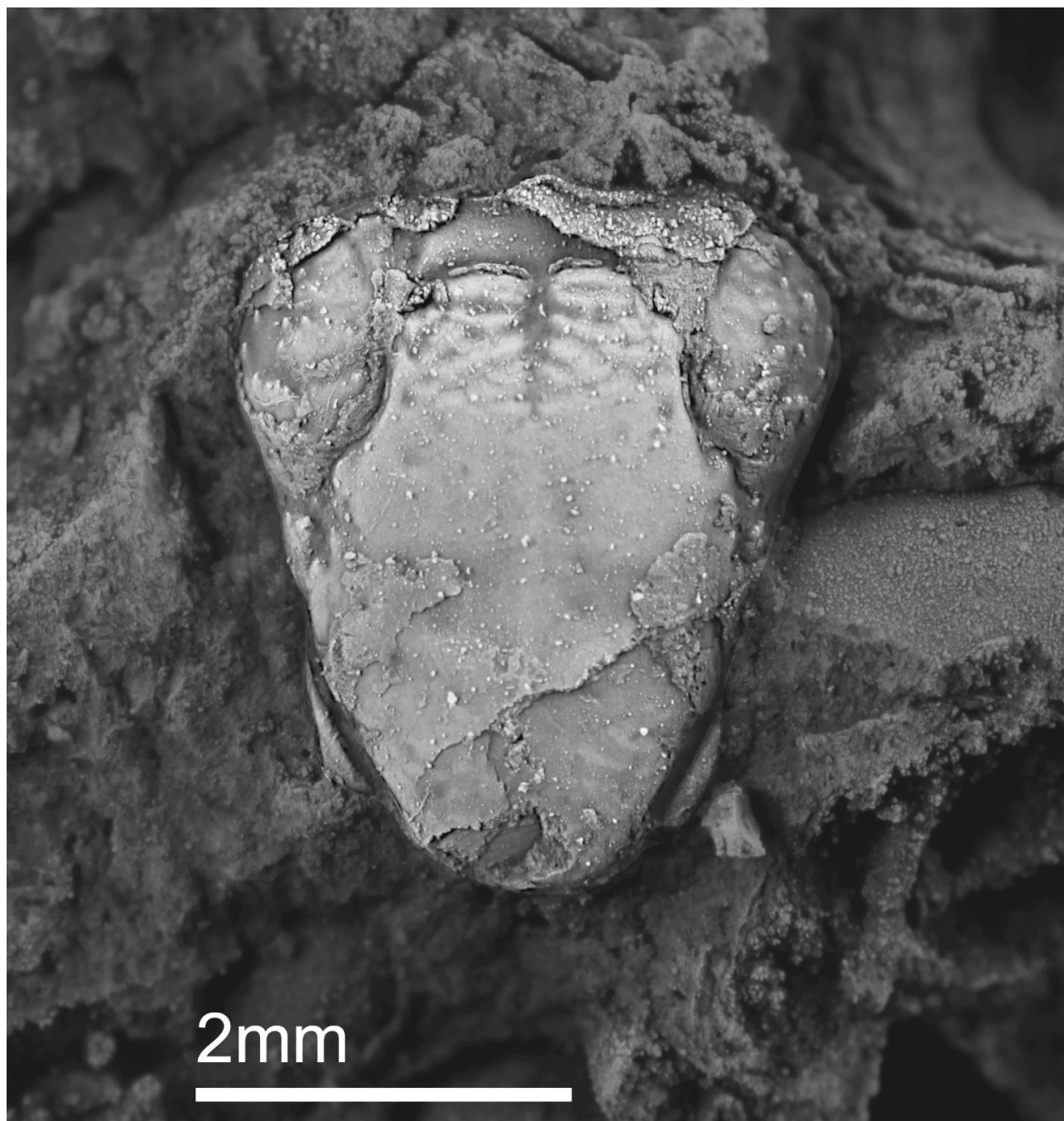


Fig. 3. Dorsal view of the shield of the holotype of *Paguristes joecollinsi* sp. nov. (MAB 10456a) as described here. No image of the lateral side is provided because the specimen sits in a depression, making further preparation too risky.

***Paguristes joecollinsi* sp. nov.**

Diagnosis: Shield elongated (length/width ratio c. 1.15); broad, rimmed and shallow orbital cavity; convex postrostral ridges indented medially by central gastric furrow; pronounced, globose and spinose massetic region; reniform keraial region; narrow and spinose lateral branchial area. Anterior gastric region with transversely crenulated muscle scar; V-shaped cervical groove.

Material: The holotype and sole known specimen to date (MAB 10456a,b: part and counter-

part) is an anterior part of the carapace with a maximum length of 3.8 mm and a maximum width of 3.3 mm.

Etymology: The species is named after our recently departed friend and colleague, Joseph ('Joe') S.H. Collins of London (England), who did so much to stimulate decapod crustacean studies by three of us (RHBF, BWMvB and JWMJ). We owe him a great deal.

Locality and stratigraphy: To the west of Kreatos Hill, about one kilometre to the north-north-west of the village of Mitsero, in coral-reef

talus of the upper Miocene (Tortonian, 11.6–7.2 Ma) Koronia Member (Pakhna Formation; see Fig. 1). The shield was recovered from a block of bioclastic rock measuring about one square metre. The sedimentology and stratigraphy of this region have been described in detail by Robertson et al. (1991) and Follows (1992).

Description: Shield elongated (L/W ratio c. 1.15), convex transversely, almost straight longitudinally, divided into distinct regions by grooves (as shown in Fig. 3); broad, rimmed and shallow orbital cavity, broad, slightly convex postrostral ridges centrally indented by central gastric furrow, extending posteriorly in faint central line; pronounced, very globose and spinose massetic region, posteriorly covered with finely spinose ridges; tiny reniform but clear keraial region; narrow and spinose lateral branchial area; anterior gastric region alongside central furrow with transversely crenulated ornament; V-shaped cervical groove; shield irregularly covered with large (setal) pores.

Remarks: The new species is assigned to *Paguristes* because the shape of the anterior shield, the grooves such as a central gastric groove, and the regional definition conform well with those of many modern species (e.g., Forest et al., 2000). Numerous representatives of *Paguristes* have been described from the fossil record, from the Albian (late Early Cretaceous) onwards (see Fraaije et al., 2015, table 1), but nearly all of these are based exclusively on chelae, with the exception of two, namely a partial shield from the upper Pleistocene of southern Italy, referred to *Paguristes* cf. *syrtensis* de Saint Laurent, 1971, by Garassino et al. (2014) and a specifically indeterminate form, *Paguristes* sp., from the lower Eocene of northern Italy (Beschin et al., 2016). A comparison with this specimen is not made here, because this species will be placed in a different genus (Fraaije et al., 2020). *Paguristes joecollinsi* sp. nov. differs from *P.* cf. *syrtensis* in having less convex orbital cavities, a much more globose massetic region, less convex upper orbital margins and substantially fewer (setal) pores across the shield, although the cuticle is less well preserved. We have also compared the species to extant representatives from the same geographical region, the Mediterranean, which was a nearly enclosed basin during the Tortonian (e.g., Rögl, 1999). After all, decapods crustaceans with stratigraphical ranges of 10 million years or more have been reported occasionally (Klompmaaker et al., 2012, p. 792–793; Hyžný, 2016, table 1). This region may also harbour one or more descend-

ants of the species in the present study. However, the shields of extant Mediterranean species of *Paguristes* are not morphologically identical or very close to the new species. *Paguristes joecollinsi* sp. nov. differs from *P. eremita* (Linnaeus, 1767) [= *P. oculatus* (Fabricius, 1775) and *P. maculatus* (Risso, 1827)] (see Pipitone, 1998; Koçak et al. 2005, for drawings and images), *P. streasensis* Pastore, 1984 and *P. syrtensis* in that the general shape is more triangular and the massetic region is more pronounced in the new species. The shield appears to show impressions of the anterior gastric muscles (sensu Klompmaaker et al., 2019, fig. 14F) in the anterior portion.

The assemblage from Mitsero also contains paguroid appendage fragments, but more research is needed to check whether one or more specimens might be ascribed to *P. joecollinsi* sp. nov. Ascribing disarticulated paguroid elements to one species is difficult, but it is essential to evaluate the true diversity of paguroids within assemblages. For example, Fraaije et al. (2013) have attempted to link sixth abdominal tergites to shield-based species based on the relative abundance of these isolated elements. None of the propodi within the Mitsero assemblage known to date is comparable to another Miocene *Paguristes*, *P. cserhatensis* Müller, 1984, from the middle Miocene of Hungary, or with *Paguristes gagnaisoni* from the middle Miocene of France (Gagnaisson, 2012).

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References

- Beschin, C., Busulini, A., Tessier, G. & Zorzin, R. 2016: I crostacei associati a coralli nell'Eocene inferiore dell'area di Bolca: Verona e Vicenza, Italia nordorientale. *Memorie del Museo civico di Storia naturale di Verona* – 2. Serie. Sezione Scienze della Terra, 9: 48–53.
- Beschin, C., Busulini, A., Calvagno, M., Tessier, G. & Zorzin, R. 2017: Ypresian decapod crustacean faunas from the coral-algal environments

- in the eastern Lessini Mountains (Vicenza and Verona territory – NE Italy): a comparative analysis. *Bulletin de la Société géologique de France*, 188/3: 13. <https://doi.org/10.1051/bsgf/2017177>
- Beschin, C., Busulini, A., Fornaciari, E., Papazzoni, C.A. & Tessier, G. 2018: La fauna di crostacei associati a coralli dell'Eocene superiore di Campolongo di Val Lione (Monti Berici, Vicenza, Italia nordorientale). *Bollettino del Museo di Storia Naturale di Venezia*, 69: 129-215.
- Buridan.over-blog.com 2018: Quelques crustacés du Danien et du Montien du Bassin de Paris. Deuxième partie (*Faxegalathea*; *Annuntidiogenes*). Accessed through: <http://buridan.over-blog.com/2018/11/quelques-crustaces-du-danien-et-du-montien-du-bassin-de-paris-deuxieme-partie.html> (on November 19, 2019).
- Dana, J. 1851: *Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe reipublicae foederatae duce, lexit et descripsit*. (Preprint from) *Proceedings of the Academy of Natural Sciences, Philadelphia* 5: 267-272.
- Dunbar, S. & Nyborg, T.G. 2003: Three specimens of hermit crabs found associated with their host gastropod shell from the Pliocene San Diego Formation, California and reassessment of the paucity of fossil hermit crabs associated with gastropod shells in the fossil record. *Geological Society of America, Abstracts with Programs*, 35: 56.
- Fabricius, J.C. 1775: *Systema Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensburg/Leipzig, Officina Libraria Kortii, 832 pp.
- Follows, E.J. 1992: Patterns of reef sedimentation and diagenesis in the Miocene of Cyprus. *Sedimentary Geology*, 79: 225-253.
- Forest, J., de Saint Laurent, M., McLaughlin, P.A. & Lemaitre, R. 2000: The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae, NIWA Biodiversity Memoir, 114: 1-250.
- Fraaije, R.H.B. 2003: The oldest *in situ* hermit crab from the Lower Cretaceous of Speeton, UK. *Palaeontology*, 46: 53-57. <https://doi.org/10.1111/1475-4983.00286>
- Fraaije, R.H.B. 2014a: Diverse Late Jurassic anomuran assemblages from the Swabian Alb and evolutionary history of paguroids based on carapace morphology. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 273/2: 121-145. <https://doi.org/10.1127/0077-7749/2014/0419>
- Fraaije, R.H.B. 2014b: A new shallow-marine mudnipsid (Anomura, Galatheoidea) from the Upper Miocene in the Maroni-Psematismenos Basin of Cyprus. In: Fraaije, R.H.B., Hyžný, M., Jagt, J.W., Krobicki, M. & Van Bakel, B.W.M. (eds.): *Proceedings of the 5th Symposium on Mesozoic and Cenozoic decapod crustaceans, Krakow, Poland, 2013: a tribute to Pál Mihály Müller*. *Scripta Geologica*, 147: 233-239.
- Fraaije, R.H.B., Artal, P., Van Bakel, B.W.M., Jagt, J.W.M. & Klompmaker, A.A. 2013: An array of sixth abdominal tergite types of paguroid anomurans (Crustacea) from the mid-Cretaceous of Navarra, northern Spain. *Netherlands Journal of Geosciences*, 92/2-3: 109-117. <https://doi.org/10.1017/S0016774600000032>
- Fraaije, R.H.B., Beschin, C., Busulini, A., Tessier, G., Jagt, J.W.M. & Van Bakel, B.W.M. 2020: *Joecalcinus*, a new hermit crab genus from the Eocene of northern Italy: the second Cenozoic representative of the family Calcinidae (Decapoda, Anomura). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* (accepted in press 13.12.2019).
- Fraaije, R.H.B., Klompmaker, A.A. & Artal, P. 2012: New species, genera and a family of hermit crabs (Crustacea, Anomura, Paguroidea) from a mid-Cretaceous reef of Navarra, northern Spain. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 263/1: 85-92. <https://doi.org/10.1127/0077-7749/2012/0213>
- Fraaije, R.H.B. & Polkowsky, S. 2016: *Dardanus colosseus*, a new paguroid from the Eocene of Austria preserved in its host gastropod shell. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 279/1: 57-62.
- Fraaije, R.H.B., Robins, C., Van Bakel, B.W.M., Jagt, J.W.M. & Bachmayer, F. 2019: Paguroid anomurans from the Tithonian Ernstbrunn Limestone, Austria – the most diverse extinct paguroid assemblage on record. *Annalen des Naturhistorischen Museum Wien*, 121: 257-289.
- Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. & Artal, P. 2008: New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 78: 193-208.

- Fraaije, R.H., Van Bakel, B.W.M., Jagt, J.W.M., Klompmaker, A.A. & Artal, P. 2009: A new hermit crab (Crustacea, Anomura, Paguroidea) from the mid-Cretaceous of Navarra, northern Spain. *Boletín de la Sociedad Geológica Mexicana*, 61/2: 211-214.
- Fraaije, R.H.B., Van Bakel, B.W.M., Jagt, J.W.M. & Machalski, M. 2015: A new hermit crab (Anomura, Paguroidea) from the upper Albian (Cretaceous) of Annopol, Poland. *Zootaxa*, 3955/4: 588-594. <https://doi.org/10.11646/zootaxa.3955.4.9>
- Gagnaison, C. 2012: Des bernard-l'hermites dans les faluns miocènes de Channay-sur-Lathan (Indre-et-Loire, France). *Cossmanniana*, 14: 67-72.
- Garassino, A., Pasini, G., De Angeli, A. & Hyžný, M. 2014: The decapod fauna (Axiidea, Anomura, Brachyura) from the Late Pleistocene of Trumbacà, Reggio Calabria (Calabria, southern Italy). *Natural History Sciences, Atti della Società italiana di Scienze naturali e Museo civico di Storia naturale di Milano*, 1/2: 119-130.
- Hyžný, M. 2016: Diversity and distribution patterns of the Oligocene and Miocene decapod crustaceans (Crustacea: Malacostraca) of the Western and Central Paratethys. *Geologica Carpathica*, 67/5: 471-494. <https://doi.org/10.1515/geoca-2016-0030>
- Karasawa, H. & Fudouji, Y. 2018: Two new species of hermit crabs (Decapoda: Anomura) from the Paleogene Kishima Group, Saga Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum*, 44: 23-28.
- Klompmaker, A.A., Feldmann, R.M. & Schweitzer, C.E. 2012: A hotspot for Cretaceous goniodromitids (Decapoda: Brachyura) from reef associated strata in Spain. *Journal of Crustacean Biology*, 32/5: 780-801. <https://doi.org/10.1163/193724012X635340>
- Klompmaker, A.A., Portell, R.W. & Frick, M.G. 2017: Comparative experimental taphonomy of eight marine arthropods indicates distinct differences in preservation potential. *Palaeontology*, 60/6: 773-794. <https://doi.org/10.1111/pala.12314>
- Klompmaker, A.A., Hyžný, M., Portell, R.W., Jauvion, C., Charbonnier, S., Fussell, S.S., Klier, A.T., Tejera, R. & Jakobsen, S.L. 2019: Muscles and muscle scars in fossil malacostracan crustaceans. *Earth-Science Reviews*, 194: 306-326. <https://doi.org/10.1016/j.earscirev.2019.04.012>
- Koçak, C., Katağan, T. & Özcan, T. 2005: Anomura of the Iskenderun Bay region (southeastern Turkey). *Crustaceana*, 78/2: 247-252. <https://www.jstor.org/stable/20107478>
- Latreille, P.A. 1802-1803: Histoire naturelle, générale et particulière, des Crustacés et des Insectes, 3. Paris (F. Dufart): 1-467.
- Lemaitre, R. & McLaughlin, P. 2019: World Paguroidea & Lomisoidea database. *Paguristes* Dana, 1851. Accessed through: World Register of Marine Species at: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=106844> on November 23, 2019.
- Linnaeus, C. 1767: *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio, 12/1, Regnum Animale, 1-2. Holmiae (Stockholm), Laurentius Salvius, pp. 533-1327.
- MacLeay, W.S. 1838: On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith A, ed. *Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa"*. London: Smith, Elder, and Co., pp. 53-71.
- Müller, P. 1984: Decapod Crustacea of the Badenian. *Geologica Hungarica, Series Palaeontologica*, 42: 1-317.
- Pastore, M. 1984: *Paguristes streasensis* n. sp. della costa Jonico-Salentina. *Thalassia Salentina*, 14: 16-27.
- Pipitone, C. 1998: *Paguristes syrtensis* de Saint Laurent, 1971 (Decapoda: Diogenidae) from the coastal waters of south western Sicily, Mediterranean Sea. *Journal of Natural History*, 32: 1741-1746. <https://doi.org/10.1080/00222939800771251>
- Risso, A. 1827: Histoire naturelle des principales productions de l'Europe méridionale et particulièrement de celles des environs de Nice et les Alpes Maritimes, volume 5. Paris/Strasbourg, F.-G. Levrault: 403 pp.
- Robertson, A.H.F., Eaton, S., Follows, E.J. & McCallum, J.E. 1991: The role of local tectonics versus global sea-level change in the Neogene evolution of the Cyprus active margin. *Special Publications of the International Association of Sedimentologists*, 12: 331-369. <https://doi.org/10.1002/9781444303896.ch19>
- Rögl, F. 1999: Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to

- Miocene paleogeography (short overview). *Geologica Carpathica*, 50/4: 339-349.
- Saint Laurent, M. de 1971: *Paguristes syrtenis*, espèce nouvelle des côtes tunisiennes (Crustacea Decapoda Diogenidae). *Bulletin du Muséum national d'Histoire naturelle de Paris*, 42/5: 1099-1107.
- Stimpson, W. 1858: *Prodromus descriptionis animalium evertebratorum, quae in expeditione ad oceanum Pacificum septentrionalem, a Republica Federate missa, Cadwaldaro Ringgold et Johanne Rodgers ducibus, obseravit et descripsit*. VII. [Preprint (December 1858) from] *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1858: 225-252. <https://doi.org/10.5962/bhl.title.51447>
- Van Bakel, B.W.M., Fraaije, R.H.B, Jagt, J.W.M. & Artal, P. 2008: An unexpected diversity of Late Jurassic hermit crabs (Crustacea, Decapoda, Anomura) in central Europe. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 250/2: 137-156. <https://doi.org/10.1127/0077-7749/2008/0250-0137>