Is Sicily an island too far for *Papilio saharae*? Why is *Papilio machaon* rushed in where *P. saharae* is feared to tread? (Lepidoptera: Papilionidae)

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Abstract. *Papilio saharae* Oberthür, 1879 (Papilionidae) was reported from Sicily on a handful of occasions in the last decade or so. On at least two instances, the taxon was claimed to have been discovered in museum collections, respectively by Moonen (2012) at the Zoological Museum, Amsterdam (ZMA) and Leraut (2016) at the Muséum National d'Histoire Naturelle in Paris. These records and a proposed nomenclatural change for *P. machaon melitensis*, were subsequently rejected by Coutsis *et al*. (2018). The present contribution provides a critique of the methodologies employed by the various authors and acknowledges that there remains much scope to investigate the *P. machaon*-complex further while maintaining that a more holistic approach is required to better understand the multidimensional dynamics that have shaped the biogeography of the central Mediterranean area.

Samenvatting. *Papilio saharae* Oberthür, 1879 (Papilionidae) werd de afgelopen tien jaar een paar keer gemeld uit Sicilië. Bij ten minste twee gelegenheden werd beweerd dat het taxon in museumcollecties was ontdekt, respectievelijk door Moonen (2012) in het Zoölogisch Museum, Amsterdam (ZMA) en Leraut (2016) in het Muséum National d'Histoire Naturelle in Parijs met daaropvolgende nomenclatuurwijziging van *P. machaon melitensis* die later werd verworpen door Coutsis *et al*. (2018). In deze bijdrage wordt kritiek geleverd op de door de verschillende auteurs gebruikte methodologieën en wordt erkend dat er nog veel ruimte is om het *P. machaon*-complex verder te onderzoeken, terwijl een meer holistische benadering nodig is om de multidimensionale dynamiek die de biogeografie van het centrale Middellandse Zeegebied heeft gevormd, beter te begrijpen.

Résumé. *Papilio saharae* (Papilionidae) a été signalé en Sicile à plusieurs occasions au cours de la dernière décennie environ. À deux reprises au moins, le taxon a été déclaré découvert dans des collections de musées, respectivement par Moonen (2012) au Musée zoologique d'Amsterdam (ZMA) et Leraut (2016) au Muséum national d'histoire naturelle de Paris avec un changement de nomenclature ultérieur qui a ensuite été rejeté par Coutsis *et al*. (2018). La présente contribution fournit une critique des méthodologies employées par les différents auteurs et reconnaît qu'il reste beaucoup à faire pour approfondir l'étude du complexe de *P. machaon*, tout en maintenant qu'une approche plus holistique est nécessaire pour mieux comprendre les dynamiques multidimensionnelles qui ont façonné la biogéographie de la région de la Méditerranée centrale.

Key words: Island biogeography — European butterfly fauna — Central Mediterranean area — Dispersal — Sympatry — Identification methods.

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Introduction

Papilio machaon Linnaeus, 1758, is an iconic species and one of the best-known members of the family Papilionidae. In terms of habitat, it is highly versatile, with a presence across two Biogeographical Regions – Palaearctic and Nearctic (including four continents – Europe, Asia, Africa, and North America) and occurring in suitable biotopes from sea-level to ≈5000 m. As a result, the *machaon*-complex has been the focus of considerable research and much has been published in both generalist and taxon-specific contributions (Oberthür 1879; Eller 1936; Seyer 1974, 1976; Higgins & Riley 1978; Clarke & Larsen 1986; Sperling 1990). In more recent times, various studies involving DNA analysis have been carried out on taxa belonging to this complex, including those that occur within the Mediterranean Basin (Sperling 1993; Sperling & Harrison 1994; Pellecchia *et al*. 2002; Vodā *et al.* 2016; Dupuis & Sperling 2020; Domagala & Lis 2022), where a number of distinct subspecies and other related taxa occur (Oberthür 1915; Tennent 1996; Tolman & Lewington 1998; Tarrier & Delacre 2008; Tshikolovets 2011). One particular taxon, which has drawn a significant attention for sharing similar morphologies is *Papilio saharae* Oberthür, 1879. This taxon has been the subject of much debate and, to some extent, also controversy.

Key issues of *P. saharae* taxon delineation history and distribution

When the taxon was described, Oberthür (1879) initially treated it as a variety of *Papilio machaon* Linnaeus, 1758 — [Original combination: *Papilo machaon* var. *saharae* Oberthür 1879, Type Locality: Laghouat (Algeria)]. Less than a decade later, he described *P. machaon hospitonoides* from a larva (Oberthür, 1888), which transpired to be that of *P. saharae* (Pittaway *et al*. 1994). While a number of individuals have treated the taxon as a subspecies, or lower, of *Papilio machaon* Linnaeus, 1758 (Seitz 1908; Turati 1924; Seyer 1986; Pellecchia *et al*. 2002), others supported the view that it was a distinct species (Pittaway 1985; Larsen 1990; Pierron 1990; Pittaway *et al*. 1994; Tennent 1996; Tolman & Lewington 1998; Tarrier & Delacre 2008; Tshikolovets 2011; Leraut 2016). Until evidence to the contrary demonstrates otherwise, the present author also subscribes to this latter viewpoint (Cassar 2018; Cassar & Catania 2022; Cassar *et al*. 2023). The species concept of *P. saharae* is grounded in evidence based on both morphology and ecology, namely, (i) the number of discernibly disparate morphological characters of all four phases of metamorphosis (Higgins & Riley 1978; Pittaway

1985; Larsen 1990; Pierron 1990; Pittaway *et al*. 1994; Tennent 1996; Tolman & Lewington 1998; Moonen 2012), and (ii) the distinctly different habitats and biotopes that the two taxa are generally known to frequent (Larsen 1983, 1990; Clarke & Larsen 1986), in part dictated by altitude (Fig. 1). Some exceptions to this latter observation are known, notably but not exclusively from the south-eastern Tunisian sahel (Pierron 1990; Cassar 2018), where Clarke & Sheppard (1956) and Larsen (1990) noted evidence of "interspecific sterility" in the Maghreb. *P. saharae* is also known from coastal localities in Libya, at Barca, Benghazi and Tripoli (Clarke & Sheppard 1956; Seyer 1974), and from locations close to the littoral in Egypt, at El Salloum (Larsen 1990) and Marsa (Gilbert & Zalat 2007). While the degree to which it maintains a sympatric presence with *P. machaon* in Libya is not altogether clear (although plausible), Gilbert & Zalat (2007) quoting Larsen, state that both taxa may occur in the Sinai. In such a case, it would presumably be *P. machaon syriacus* as opposed to *P. machaon mauretanica* further west. The topic of natural zones of contact across the Maghreb and the eastern Mediterranean, including the Levant, and resultant interbreeding and hybridization is treated in quite some detail by Benyamini & John (2020). In the context of hybridization, also refer to Cassar *et al.* (2023), in which *Papilio saharae aferpilaggi* Cassar, Catania & Cotton 2023 was described from the central Mediterranean island of Lampedusa.

In 2012, a record of *P. saharae* came to light when museum specimens (at the time at the Zoological Museum, Amsterdam — ZMA) were being curated (Moonen 2012). The specimen in question, a male, was taken in Lentini in Sicily, by H. van Oorschot, in September of 1978. Consequently, Leraut (2016) claimed to have discovered several specimens of *P. saharae* also taken in Sicily, in the collections of the Muséum National d'Histoire Naturelle in Paris. Patrick Leraut provides no details on the specimens' field data nor on the morphological characters used and/or methodology employed to determine them. He also proposed that *P. machaon melitensis*, the taxon that occurs exclusively in Malta, be referred to as *P. saharae melitensis* Eller, 1936. The author apparently based his assessment on photographed material from the Internet (Rennwald 2021); however, as in the case of the Paris Museum specimens, he offered no scientific basis for this assertion. Coutsis *et al*. (2018) reacted to Moonen's (2012) record and Leraut's findings (2016), rejecting the notion of any presence of *P. saharae* in Europe. However, their conclusions were based on what appears to be a rather small sample size (even if the precise number of voucher specimens examined is not divulged). In an updated checklist of European butterflies, Wiemers *et al*. (2018) omitted any mention of *P. saharae*, the reason for which was undisclosed.

In the same year, Cassar (2018) reported a specimen from Giarratana in Sicily with a number of morphological characters akin to those of *P. saharae*; regrettably, an examination of the harpe (Fig. 2) was not an option, given it was a female specimen. Intriguingly, both Giarratana and Lentini lie on the Hyblean plateau, that is, the south-eastern portion of Sicily that effectively forms part of the emergent segments of the Pelagian Block (= foreland margin of the African plate boundary). Moreover, although the environment of these localities is generally semi-arid, it tends to become significantly more arid in areas of exposed terrain with shallow soils, particularly during the dry season (Cassar 2018).

Connectivity for dispersal

Island environments continue to provide an opportunity for biogeographical research since insularity is often a key driver in defining the biotic structure of island communities (Cassar & Pisani 2021). Insular systems can also provide some rather useful insights into natural processes, distribution patterns, and dispersal dynamics (Quammen 1996), particularly in relation to habitat fragmentation (Drake *et al*. 2002). Evolutionary development and subsequent speciation are typically influenced by a population's capacity to adapt to unfamiliar environmental conditions, coupled with sustained isolation from the species' centre of origin (Lomolino 2000). The biogeographical importance of the central Mediterranean area, comprising the marine causeway between northern Africa and southern Europe (specifically the Sicily Channel between the Siculo-Tunisian Sill and the eastward area encompassing the Pelagian Block), cannot be overstated.

A complex combination of geo-tectonics and climate-induced fluctuations in eustatic sea-levels during the late Miocene (Hsü 1983; Krijgsman *et al*. 1999; Gargani & Rigollet 2007) and later, during the Pleistocene epoch, provided the mechanism for dispersal of terrestrial biota through ecological corridors that formed intermittently during episodes of marine regressions (Massa 1982; Hunt & Schembri 1999; Cassar *et al*. 2007; Cassar & Pisani 2021). It is within the framework of such dynamic complexity that the biogeography of species, including that of *P. saharae*, needs careful consideration; most certainly, it should not be consigned to a 'polar interrogative' yes/no question, rendering what ought to be an objective scientific investigation, a simplistic box-ticking exercise. This is the key issue that the present contribution shall in part endeavour to address.

Aims

This paper is not intended to address the vexed question of whether *P. saharae* is present in Sicily or, if it indeed it is, how and when it reached the Mediterranean's largest island; nor does it set out to address its merited taxonomic rank. Rather it aims to revisit and discuss the respective methodologies employed by Moonen (2012), Leraut (2016) and Coutsis *et al*. (2018), while acknowledging that there remains scope to investigate the biogeography of the *P. machaon*-complex in the central Mediterranean area (including the north African mainland) taxonomically, through both morphometrics and molecular analysis.

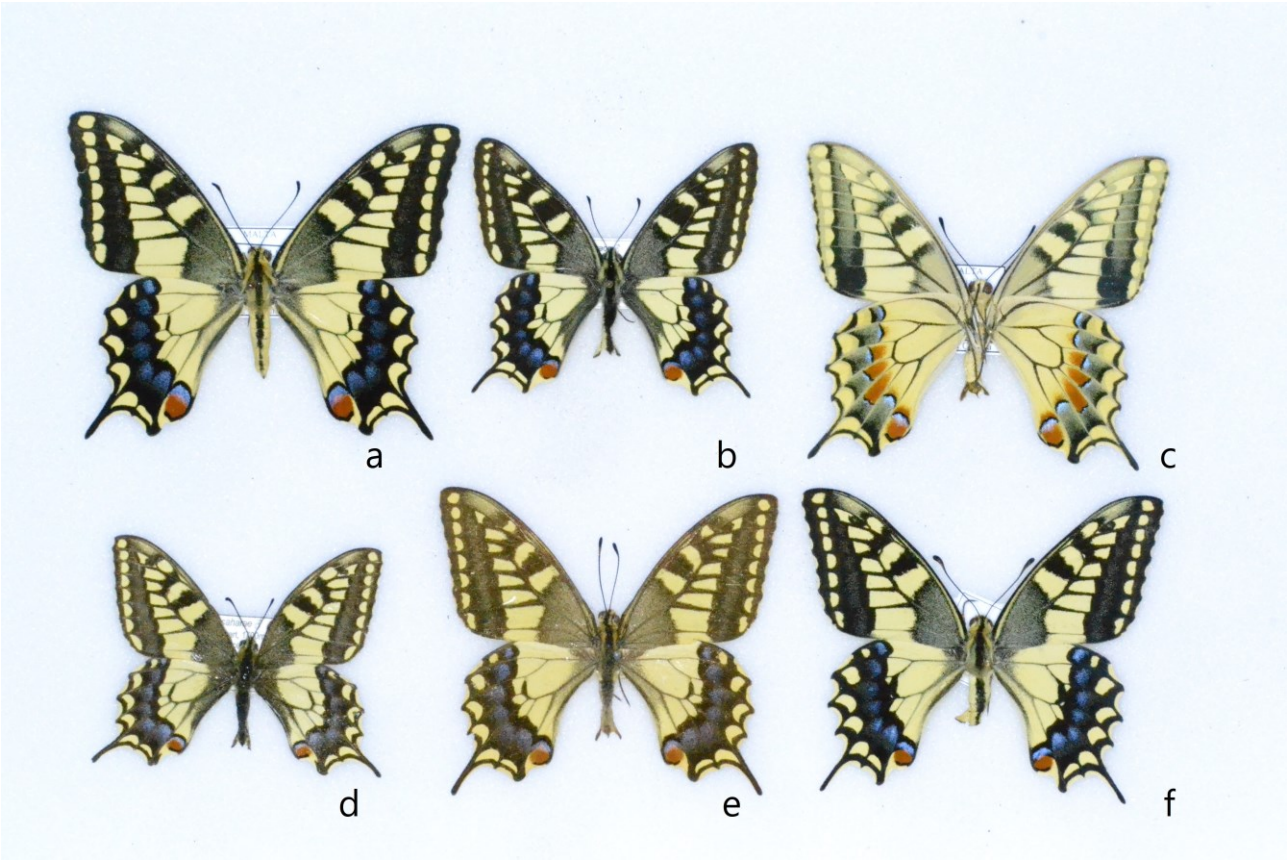

Fig. 1. Upper row: a, *Papilio machaon melitensis*, MALTA, *loc.* Kuncizzjoni, 190 m, ♂ 15.ix.2021 (Coll. AC); b, *loc.* Zebbug, 60 m, ♂ 13.v.2019 (Coll. LFC); d, *loc.* Kuncizzjoni, 190 m, ♂ 15.ix.2021 (Coll. AC). This taxon, as is common with a number of other related subspecies, demonstrates significant size disparity among adults, with variance not exclusively a function of seasonality or concentration of available larval food sources. The dimensions of adult individuals of mutual broods (inclusive of bred siblings) are also known to vary appreciably.

Lower row: d, *Papilio saharae saharae*, MOROCCO, *loc.* Tizi-Tazouguart, 1150 m, ♂ 19.iv.2018 (Coll. LFC); e, *Papilio machaon sphyrus*, ITALY, Sicily, *loc.* Adrano, Mt. Etna, 560 m, ♂ 22.vii.1979 (Coll. LFC); f, *loc.* Il Pagliaio delle Madonie, 1036 m, ♂ 14.vi.2019 (Coll. AC). [Deposited in the collections of Louis-F. Cassar or A. Catania]. © Aldo Catania.

Discussion

The diversity of habitats within which the taxon occurs is well documented. *P. saharae* is not a species that is restricted exclusively to eremic environments as is commonly assumed. The nominotypical *P. saharae saharae*, the range of which extends from Morocco to the Red Sea and beyond into the northern Hejaz, is known from hyper-arid zones on the northern fringes of the Sahara Desert, as well as from arid steppe and semi-arid plains closer to the Mediterranean coast, where zones of contact with *P. machaon* are known to occur (Clarke & Sheppard 1956; Seyer 1974; Larsen, 1990; Pierron 1990; Gilbert & Zalat 2007; Cassar 2018; Benyamini & John 2020). *P. saharae rathjensi*, the subspecies from Yemen and the Asir region in Saudi Arabia, is typically found around mesic habitats within rocky uplands and montane zones (Larsen 1983, 1984, 1990; Pittaway 1985; Meerman & Boomsma 1986).

Although preferences relating to habitat and biotope-types as well as flight period have often been alluded to as distinguishing features to separate the two taxa (Larsen 1990; Pittaway *et al*. 1994; Tennent 1996; Tolman & Lewington 1998; Moonen 2012), various records have demonstrated instances which digress from the typical 'dry' for *P. saharae* and 'temperate' for *P. machaon* composition, especially where the two taxa occur sympatrically and where their respective favoured climatic zones tend to grade into one another without clearcut delineation (Larsen 1990; Pierron 1990; Gilbert & Zalat 2007; Cassar 2018; Cassar & Catania 2022). It also seems that both *P. machaon* and *P. saharae* can produce a number of generations across seasons when conditions are suitable, even if it has been noted that *P. saharae* broods are quite dependent on annual patterns of precipitation (Pittaway *et al*. 1994). Given such a scenario, might there be instances where *P. saharae* is exploiting *ecological refugia* in enclaves supporting environmentally suitable, albeit fragmented, biotopes, but also dispersing onto adjacent, more temperate zones? Recent field research within the central Mediterranean area has revealed interesting new insights on the adaptation of *P. saharae* to semi-arid environments (Cassar & Catania 2022; Cassar, Catania & Cotton 2023).

The critique that follows identifies some insufficiencies in the approaches employed to assess the presence of *P. saharae* in southern Europe. Perhaps one of the first errors of judgement occurred when Moonen (2012) did not broaden his investigation to include an examination of the genitalia of the male specimen encountered during

Fig. 2. Harpe; a, *Papilio saharae saharae*; b, *P. machaon sphyrus*; c, *P. machaon melitensis*. © Aldo Catania.

the curation exercise at the ZMA. Had he not fallen short of counting the teeth on the harpe, one of the more critical characteristics for defining *P. saharae*, the identity of the specimen would have been settled beyond question and the issue of distribution conclusively laid to rest. Of course, such an omission does not diminish the likelihood of the taxon's presence in Sicily but may give rise to doubts amongst those sceptical of such occurrence. A few years following the Moonen publication, Leraut (2016) made a somewhat extraordinary claim of having come across a number of Sicilian specimens in the collections of the museum in Paris that, according to the author, were erroneously determined as *P. machaon* but which he identified as *P. saharae*. Unfortunately, he provided no specifics, either of locality or biometric data, nor of his approach to determining the said specimens. Had such data and method been included, Leraut's findings could potentially be considered more reliable. Perhaps even more remarkable was his declaration that *P. machaon melitensis*, the subspecies present on the Maltese Islands, should be referred to as *P. saharae melitensis* Eller, 1936. Apparently, Leraut based his determination on photographed pinned butterfly specimens on the Internet (Rennwald 2021), which may or may not have had a scale bar or other taxa of the *machaon*-complex for comparative purposes. It may also be pertinent to add that the Malta taxon was molecularly analysed in the past (Vodă *et al*. 2016) and nothing unpredicted was reported. Coutsis *et al*. (2018), who published some interesting lab-work results involving artificial hybridisation between *P. machaon* and *P. saharae*, rejected Moonen's record and all of Leraut's claims and suggestions. The issue with the view held by Coutsis *et al*. (2018) is that the authors based their decision on the examination of a handful of specimens from Sicily and Malta (the precise number of which was never divulged) which they compared with *P. saharae* from the Negev desert in Israel. Perhaps, had the museum specimens referred to by Moonen (2012) and Leraut (2016) been re-examined, the issue would have been resolved.

More significantly, the foregoing highlights the fact that related investigations need to be broadened, to incorporate a thorough understanding of the biogeography of the taxa in question, particularly with reference to the rather complex geo-tectonic and climate-induced eustatic sea-level fluctuations that had a profound influence on dispersal patterns and biotic make-up within the central Mediterranean area. In the absence of such a holistic and integrated approach, any conclusions, i.e., that *P. saharae* should be excluded from the fauna of Sicily, are highly debatable, if not distinctly unconvincing. At this juncture, it may be apposite to add that in May of 2018, the present author took a female specimen at Giarratana in Sicily (not too distant from Lentini, where the Moonen specimen was taken), which had a number of discernible morphological characters common to *P. saharae*, notably, 31 antennal segments, a compressed vannal fold with a small red ovoid ocellus and an evident smattering of yellow scales over the dark markings of the forewing basal and postbasal areas and the hindwing basal and inner margin regions (Cassar 2018). The contribution discusses the potential of a relict population of *P. saharae*, as well as various scenarios concerning dispersal, sink and source dynamics, past and present environmental conditions, and the multifarious processes that influenced biotic make-up as a consequence of Quaternary Period climate-induced changes in some detail.

Conclusions

Opportunities for dispersal are highly likely to have existed in the past, particularly during Quaternary lowstands, while *P. saharae*'s ability to thrive in less arid environments has been demonstrated on numerous occasions by various authors (cited above). So why disavow the notion of the species' presence in southern Europe? Notwithstanding the fact that islands tend to make poor targets (compared to continental landmasses) for immigrant organisms, the extensive length of the Sicilian coastline, coupled by the significantly shorter distance across the Siculo-Tunisian strait during the Quaternary Period, it is certainly not implausible that non-migrant species such as *P. saharae* made landfall and successfully adapted to Sicily's semi-arid environment.

In summary, the key takeaway of the message presented above is the value of a holistic and sound methodological design, and the questions it raises for future research on the distribution and status of *Papilio saharae* in the central Mediterranean area. An integrated approach towards understanding the biogeography of the species can not only shed light on phylogenetic relationships with other taxa, but also provide vital evidence of past environments and climates, including

landform and associated dynamics, in this case, of the central Mediterranean area. Such knowledge, coupled with a thorough understanding of the taxon's distribution patterns and its capacity to adapt to different habitats, is crucial to any effort to apply conservation measures that may ensure the species' long-term survival. Finally, the present author would like to emphasize that the intention of this contribution is not that of censorship and that any perceived criticism is intended to objectively improve current knowledge.

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References

Benyamini D. & John E. 2020. *Butterflies of the Levant and nearby areas*. Vol. II: *Papilionidae, Pieridae & Hesperiidae*. 4D MicroRobotics Publications Ltd. 208 pp.

Cassar L.-F. 2018. *Papilio saharae* Oberthür, 1879 (Lepidoptera Papilionidae) on the Hyblean Plateau, Sicily: Case of a relict population due to climate-driven phenomena? — *Naturalista siciliano* **42**(1): 21–29.

Cassar L.-F. & Pisani C.M. 2021. A follow-up cycle of observations on the endemic *Pamphagus ortolanii* (Acridoidea Pamphagidae). — *Naturalista siciliano* **45**(1–2): 237–246.

Cassar L.-F. & Catania A. 2022. Preliminary findings on the presence of a taxon with morphological traits of *Papilio saharae* Oberthür, 1879 in Lampedusa (Italy) (Lepidoptera: Papilionidae). — *SHILAP Revista de lepidopterología* **50**(198): 303–312.

Cassar L.-F., Catania A. & Cotton A. M. 2023. A new subspecies of *Papilio saharae* Oberthür, 1879 (Lepidoptera: Papilionidae) from Lampedusa, Italy. — *Zootaxa* **5231**(1): 065–078.

Clarke C. A. & Larsen T. B. 1986. Speciation problems in the *Papilio machaon* group of butterflies. — *Systematic Entomology* **11**: 175–181.

Coutsis J. G., Anastassíu H. & Benyamini D. 2018. About the recently published records of *Papilio saharae* from Sicily and Malta (Lepidoptera: Papilionidae). — *Phegea* **46**(4): 132–136.

Domagala P. A. & Lis J. A. 2022. One species, hundreds of subspecies? New insight into the intraspecific classification of the Old World swallowtail (*Papilio machaon* Linnaeus, 1758) based on two mitochondrial DNA markers. — *Insects* **13:** 752.

Drake D. R., Mulder C. P. H., Towns D. R. & Daugherty C. H. 2002. The biology of insularity: an introduction. — *Journal of Biogeography, Special Issue: Insular Biotas* **29**(5/6): 563–569.

Dupuis J. R. & Sperling F. A. H. 2020. Phylogenomic test of mitochondrial clues to archaic ancestors in a group of hybridizing swallowtail butterflies. — *Molecular phylogenetics and evolution* **152**: 106921.

Gargani J. & Rigollet C. 2007. Mediterranean Sea level variations during the Messinian Salinity Crisis. — *Geophysical Research Letters* **34**(10): L10405.

Gilbert F. & Zalat S. 2007. *Butterflies of Egypt: Atlas, Red Data Listing, & Conservation*. Nature Conservation Sector, Egyptian Environmental Affairs Agency, 183 pp.

Higgins L. G. & Riley N. D. 1978. *Die Tagfalter Europas und Nordwestafrikas*. — Verlag Paul Parey, Hamburg, Berlin, 377 pp.+60 pl.

Hsü K.J. 1983. *The Mediterranean was a Desert*. — Princeton University Press, Princeton, New Jersey. 197 pp.

Hunt C. O. & Schembri P. J. 1999. Quaternary environments and biogeography of the Maltese Islands. — *In*: Mifsud A. & Savona Ventura C. (eds.), *Facets of Maltese prehistory*. — The Prehistoric Society of Malta, Malta, 41–75 pp.

Krijgsman W., Hilgen F.J., Raffi I., Sierro F.J. & Wilson D. S. 1999. Chronology, causes and progression of the Messinian salinity crisis. — *Nature* **400**(6745): 652–655.

Larsen T. B. 1984. The zoogeographical composition and distribution of Arabian butterflies (Lepidoptera; Rhopalocera). — *Journal of Biogeography* **11**: 119–158.

Larsen T. B. 1990. *The Butterflies of Egypt*. Apollo Books, American University Press, Cairo, 112 pp.+8 pl.

Leraut P. 2016. *Butterflies of Europe and neighbouring regions*. *N.A.P Ed*., Verrières-le-Buisson, 1113 pp.+ 655 pl.+ 6000 photos.

Lomolino M. V. 2000. A Call for a New Paradigm of Island Biogeography. — *Global Ecology and Biogeography* **9**(1): 1–6.

Massa B. 1982. Il gradiente faunistico nella penisola Italiana e nelle Isole. *Atti della Società Italiana di Scienze Naturali* e *del Museo Civico di Milano* **123**: 353–374.

Meerman J. & Boomsma T. 1986. The little-known swallowtail from northern Yemen, *Papilio saharae rathjensi* Warnecke 1932 — Field observations and breeding (Lepidoptera: Papilionidae). — *Entomological Journal* **96**(13): 177–182.

Moonen J. J. M. 2012. Notes on the *Papilio machaon* group (Lepidoptera: Papilionidae) from the Palaearctic Papilionidae collection of the Zoological Museum of Amsterdam. — *Entomological Reports* **72**(3): 184–186.

Oberthür C. 1879. Catalogue raissoné des Papilionidae de la collection de Ch. Oberthür. — *Études d'Entomologie* **4**: 19–102, 107–117, pls. I–VI. https://www.biodiversitylibrary.org/page/10180732

Oberthür C. 1888. Faunes Entomologiques. Descriptions d'insectes nouveaux ou peu cunnus. III. Lépidoptères d'Europe et d'Algérie. — *Études d'Entomologie* **12**: 21–46. https://www.biodiversitylibrary.org/page/10426455

Oberthür C. 1915. Faune des Lépidoptères de la Barbarie. — *Études de Lépidoptérologie comparée* **10**: 7–459, pl. 276–297, 301, 302, 306–309. https://www.biodiversitylibrary.org/page/9648659

Pellecchia M., Marini M. & Scali V. 2002. Diversità mitocondriale nel *Papilio machaon* species complex (Papilionidae): evidenze dai geni CO I e NADH 4. — *Atti XIX Congresso Nazionale Italiano di Entomologia,* 131–134.

Pierron M. 1990. Contribution a la connaissance de la biologie de *Papilio machaon saharae* Obth. Differences avec *Papilio machaon machaon* L. et hybridations experimentales (Lep. Papilionidae). — *Alexanor* **16**(6): 331–340.

Pittaway A. R. 1985. Lepidoptera Rhopalocera from western Saudi Arabia. — *Fauna of Saudi Arabia* **7**: 172–197.

Pittaway A. R., Larsen T. B., Clarke C. A., Smith C. R., Crnjar R. & Clarke F. M. M. 1994. *Papilio saharae* Oberthür, 1879, specifically distinct from *Papilio machaon* Linnaeus, 1758 (Lepidoptera: Papilionidae). — *Entomologist's Gazette* **45**(4): 223–249.

Quammen D. 1996. *The Song of the Dodo: Island Biogeography in an Age of Extinctions*. Scribner, New York, 702 pp.

Rennwald E. 2021. Aid for determining the butterfly species found in Europe. *Papilio saharae* Oberthür, 1879. Version 17. Last modified by Jürgen Rodeland on November 14, 2022. https://lepiforum.org/*Papilio_saharae* (accessed 22 December 2022).

Seitz A. 1907–1909. Grossschmetterlinge der Erde, Vol. 1, Die palaearktischen Tagfalter. — A. Kernen Verlag, Stuttgart. 379 pp. + 89 pls + 3470 figs. https://www.biodiversitylibrary.org/page/10122597

Seyer H. 1974. Versuch einer Revision der *Papilio machaon* subspezies in der westlichen Paläarktis. — *Mitteilungen der Entomologischen Gesellschaft Basel* **24**: 64–90, 93–117.

Seyer H. 1986. Zum taxonomischen Status von *Papilio machaon saharae*. — *Entomologische Zeitschrift* **96/18**: 270.

Sperling F. A. H. 1990. Natural hybrids of *Papilio* (Insecta: Lepidoptera): poor taxonomy or interesting evolutionary problem? — *Canadian Journal of Zoology* **68**(8): 1790–1799.

Sperling F. A. H. 1993. Mitochondrial DNA phylogeny of the *Papilio machaon* species group (Lepidoptera: Papilionidae). — *Memoirs of the Entomological Society of Canada* **125**(S165): 233–242.

Sperling F. A. H. & Harrison R. G. 1994. Mitochondrial DNA variation within and between species of the *Papilio machaon* group of swallowtail butterflies. — *Evolution* **48**(2): 408–422.

Tarrier M. R. & Delacre J. 2008. *Les papillons de jour du Maroc. Guide d'identification et de bioindication*. — Muséum national d'Histoire naturelle, Paris; *Biotope*, Mèze, 480 pp.

Tennent J. 1996. *The Butterflies of Morocco, Algeria and Tunisia*. — Gem Publishing Co., xxxvi + 217 pp.

Tolman T. & Lewington R. 1998. *Die Tagfalter Europas und Nordwestafrikas, übersetzt von M. Nuß*, Franckh-Kosmos. — Verlags-GmbH & Co., Stuttgart, 319 pp.

Tshikolovets V. V. 2011. *Butterflies of Europe & the Mediterranean area*. — Tshikolovets Publications, Kyiv, 544 pp.

Turati E. 1924. Spedizione Lepidopterologica in Cirenaica 1921–22. — *Atti della Società Italiana di Scienze Naturali* **63**: 21–129.

Vodă R., Dapporto L., Dincă V., Shreeve T. G., Khaldi, M., Barech G., Rebbas K., Sammut P., Scalercio S., Hebert P. D. & Vila R. 2016. Historical and contemporary factors generate unique butterfly communities on islands. — *Scientific Reports* **6**: 1–11.

Wiemers M., Balletto E., Dincã V., Fric Z. F., Lamas G., Lukhtanov V., Munguira M. L., Swaay C. A. M. van, Vila R., Vliegenthart A., Wahlberg N. & Verovnik R. 2018. An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). — *ZooKeys* **811**: 9–45. https://zookeys.pensoft.net/article/28712/