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A Triassic spider from Italy

FABIO M. DALLA VECCHIA and PAUL A. SELDEN

A new fossil spider from the Triassic (Norian) Dolomia di Forni Formation of Friuli, Italy, is described as *Friularachne rigoi* gen. et sp. nov. This find brings the number of known Triassic spider species to four. The specimen is an adult male, and consideration of various features, including enlarged, porrect chelicerae, subequal leg length, and presence of a dorsal scutum, point to its identity as a possible member of the mygalomorph superfamily Atypoidea. If correct, this would extend the geological record of the superfamily some 98–115 Ma from the late Early Cretaceous (?Albian, c. 100–112 Ma) to the late middle–early late Norian (c. 210–215 Ma).

Introduction

Triassic spiders are extremely rare. Only three have hitherto been described: a mygalomorph from the Grès à Voltzia of France (Selden and Gall 1992) and araneomorphs from Virginia and South Africa (Selden et al. 1999, 2009). Here, we describe a single specimen of a new spider from the Triassic (Norian) Dolomia di Forni Formation of Friuli, north-east Italy. It possibly belongs to the mygalomorph superfamily Atypoidea, and the discovery would extend the fossil record of the superfamily by some 98-115 Ma from the previous oldest record in the late Early Cretaceous (Eskov and Zonshtein 1990). Atypoids occur widely across the Palaearctic, Nearctic, and Afrotropical zoogeographic regions at the present day; the new fossil find suggests that the superfamily could have already been widespread across Pangaea in Triassic times. Recent atypoids live permanently in their webs or burrows except when dispersing as juveniles or as wandering adult males. The fossil is an adult male found in a marine depositional environment so, assuming that it had a similar mode of life to Recent atypoids, this is consistent with the specimen having been washed into the sea while wandering in search of a mate.

Institutional abbreviations.—MFSN, Museo Friulano di Storia Naturale, Udine, Friuli, Italy.

Geological setting

The specimen comes from the Rovadia Brook valley on the north slope of the Carnian Prealps, Forni di Sopra Municipality, Friuli Venezia Giulia Region, north-east Italy (Fig. 1A). It is preserved on a slab of black dolostone collected in debris in the bed of the brook. The flanks of the valley are made entirely of the Dolomia di Forni Formation (Carulli et al. 2000), and the rock preserving the spider is characteristic of this formation.

The Dolomia di Forni Formation is a sequence of dark grey to black or brown, well-bedded, bituminous dolostone with chert, 700–850 m thick (Carulli et al. 2000 and references therein). It crops out as an east to west band for over 30 km in the Carnic Prealps of the Friuli Venezia Giulia region (Fig. 1A) and is a lateral equivalent to the Dolomia Principale Formation (= Hauptdolomit of German authors). It represents deposition in an anoxic marine basin whose maximum depth was about 400 m, and was surrounded by the shallow water carbonate platform of the Dolomia Principale Formation (Carulli et al. 1997; Scotti et al. 2002). The basin originated by tensional tectonics at the western end of the Pangean Gulf of Tethys (Gaetani et al. 2000).

The age of the Dolomia di Forni Formation is late middle to early late Norian (late Alaunian–early Sevatian) based on its conodont content (Roghi et al. 1995; Carulli et al. 2000; Moix et al. 2007; Dalla Vecchia 2008). Since the Norian–Rhaetian boundary probably falls in the 207–210 Ma time interval (Muttoni et al. 2010), the specimen here described is somewhat older, possibly 210–215 Ma (Fig. 1B).

The Dolomia di Forni Formation has yielded a peculiar fossil assemblage composed mainly of decapod crustaceans (Garassino et al. 1996; Garassino 2000), thylacocephalans (Dalla Vecchia and Muscio 1990; Arduini 1992), terrestrial plant remains (Dalla Vecchia 2012), marine fishes (Dalla Vecchia 2008; and references therein), and terrestrial tetrapods (Dalla Vecchia 2006; and references therein) including some of the oldest pterosaurs (Dalla Vecchia 2009a, b). Most of those fossils, including the archosauromorph Megalancosaurus preonensis and the pterosaur Preondactylus buffarinii, come from the Seazza Brook valley near Preone village, which occurs east of the Rovadia Brook valley (Fig. 1A). The Rovadia Brook section has also yielded remains of decapod crustaceans (benthic and nectonic; FMDV personal observations), marine fishes (Dalla Vecchia 2008), terrestrial plants (Dalla Vecchia 2012), the protorosaurian Langobardisaurus (Renesto et al. 2002), and a pterosaur (Dalla Vecchia 2000).

The terrestrial plants and tetrapods (Dalla Vecchia 2002), and the composition of the organic matter (Scotti et al. 2002) testify to the presence of emergent parts of the carbonate platform close to the marine basin. Thus, a terrestrial spider is not unexpected, despite its preservation in marine deposits. It could have been transported into the sea by tidal currents, storms or hurricanes, or on floating plant remains.

Plants represent a high percentage of the fossil assemblage, but show a low diversity, being represented mainly by small shoots of the Coniferales genus-forms *Brachyphyllum–Pagiophyllum*, and large, isolated leaves that are characteristically narrow, elongated and pointed (Dalla Vecchia 2012) and possibly referable to the genus *Pelourdea* (Evelyn Kustatscher, personal communication to FMDV 2011). A palynological sample has given only pollens belonging to cheirolepidiacean and araucariacean Coniferales

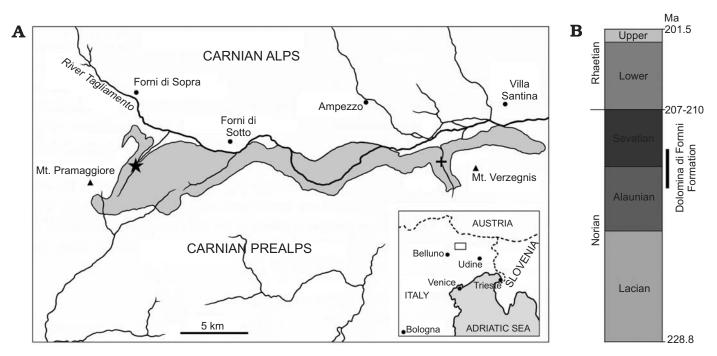


Fig. 1. **A.** Location of the discovery locality along the Rovadia Brook valley (star). The extent of the Dolomia di Forni outcrop is in grey; the cross indicates the position of the Seazza Brook near Preone village. **B**. Chronostratigraphic range of the Dolomia di Forni Formation, based on its conodont content. The age of the Rhaetian–Hettangian and Norian– Rhaetian boundaries are from Muttoni et al. (2009), that of the Carnian–Norian boundary is from Ogg et al. (2008).

(Carulli et al. 2000). The dominance of the Coniferales and narrow-leafed plants is typical of a xeric flora and is indicative of a relatively dry, warm climate like that existing today along the coasts of the Persian Gulf. This is supported also by the tropical location of the region during the Triassic (Gaetani et al. 2000), the widespread early (syndiagenetic) dolomitization of the carbonate sediment both in the platform (Frisia 1994) and in the basin (Mattavelli and Rizzini 1974), the absence of structures related to tropical karstification in the emergent platform (Frisia 1994), and the sporadic presence of evaporitic minerals in the intraplatform basins (Mattavelli and Rizzini 1974; Cozzi 2000).

Material and methods

The single specimen (MFSN40302a and b; part and counterpart respectively) was studied, drawn and photographed in MFSN, using a Leica MZ8 stereomicroscope and a Canon EOS 5D Mk II camera. The fossil was mainly studied under ethanol to enhance the contrast between the specimen and the matrix. Mosaics of high-resolution images were merged into single images of the whole part and counterpart using Adobe Photoshop CS5 Extended software. Drawings were constructed using Adobe Illustrator CS5. Measurements of the specimen were difficult because of the poor preservation; these were made from the images using Photoshop. Measurements given below in the Systematic palaeontology chapter are the means of both left and right, part and counterpart, and are in mm.

Interpretation of the fossil

Taphonomy.—The spider is preserved as dark brown material (presumably organic matter) in a fine-grained dolostone. In the

region of the opisthosoma is an elliptical patch of thick, black material which resembles carbon. Generally in fossil arthropods, the darkness of the brown colouration reflects the thickness of the organic matter, and therefore that of the original cuticle. The leg measurements differ left to right because more of the basal parts are exposed from beneath the carapace on the right side of the part (MFSN40203a; Fig. 2A); this is because the body has shifted to the left slightly during compaction.

Morphological interpretation.—The anterior part of the carapace appears darker, where it is presumably thicker and bears some lobes which could be the remains of the eye tubercle and eyes, or just a lobed region. This area is wide, and suggests a broad, blunt anterior border to the carapace. Laterally and posteriorly, the edges of the carapace are poorly defined. The dark oval patch on the opisthosoma most likely represents a scutum. Beyond the scutum there is a pale oval area which may correspond to the true extent of the opisthosoma; this is outlined in the figures with dashed lines. Alternatively, this pale area could represent a colour change in the matrix due to some other cause, such as exudate from the fossil during diagenesis. The chelicerae are rather dark in colour, being composed of thick cuticle. They extend far out anteriorly from the front of the carapace. At least the base of a presumed fang can be seen on the counterpart (MFSN40302b, Fig. 3), as well as some dark spots which could represent cheliceral denticles. The left chelicera on the counterpart (MFSN40302b) could be interpreted as somewhat fatter and compressed to the left (see Fig. 3). The pedipalps are clearly expanded distally, which indicates that the specimen is an adult male; a dorsal abdominal scutum is also a common feature of adult males in some spider families.

Systematic palaeontology

Order Araneae Clerck, 1757 Suborder Opisthothelae Pocock, 1892 Infraorder Mygalomorphae Pocock, 1892 ?Superfamily Atypoidea Thorell, 1870 Genus *Friularachne* nov.

Type species: Friularachne rigoi sp. nov., monotypic; see below. *Etymology:* After the Friuli region of Italy (Friûl in the Friulian language) where the fossil was found, and Greek, *arachne*, a spider.

Diagnosis.—Atypoid-like spider with a carapace broadening anteriorly; single dorsal scutum extending more than half the length of the opisthosoma (at least in the adult male); large, porrect chelicerae with denticles on both pro- and retromargins; legs relatively long and thin.

Remarks.—This diagnosis is necessarily descriptive, rather than comparative, because of the uncertainty surrounding the true identity of the spider.

Friularachne rigoi sp. nov. Figs. 2, 3. *Etymology*: In honour of the finder, Roberto Rigo, Udine, Italy. *Holotype*: MFSN40302a (part) and MFSN40302b (counterpart), moder-

Type locality: Rovadia Brook valley, Forni di Sopra municipality, Udine Province, Friuli Venezia Giulia Region, Italy.

Type horizon: Dolomia di Forni Formation, upper Alaunian–lower Sevatian (upper middle–lower upper Norian).

Diagnosis.—As for the genus.

ately well preserved adult male.

Description.—Adult male. Body length (excluding chelicerae) 3.48 mm; carapace length 1.41 mm, width 1.27 mm (L/W ratio 1.11); broad, straight anterior margin with frontal (ocular?) lobes. Chelicera length 0.78 mm; subelliptical shape in dorsoventral view; fang emerging from distal end, apparently at least half length of paturon; denticles possibly present on paturon adjacent to fang. Pedipalp length 1.05 mm; proximal podomeres slender, swollen tarsus (adult male). Leg podomere lengths: leg 1 femur 1.44 mm, patella 0.28 mm; leg 2 femur 1.18 mm, patella 0.41 mm, tibia 0.62 mm; leg 3 femur 1.10 mm, patella 0.32 mm, tibia 0.67 mm, metatarsus 0.83 mm, tarsus 0.56 mm; leg 4 femur 1.13 mm, patella 0.35 mm, tibia 0.60 mm, metatarsus 0.96 mm, tarsus 0.55 mm. Leg formula (longest to shortest) 1243? Opisthosoma length 2.10 mm, width 1.13 mm (L/W ratio 1.87); single,

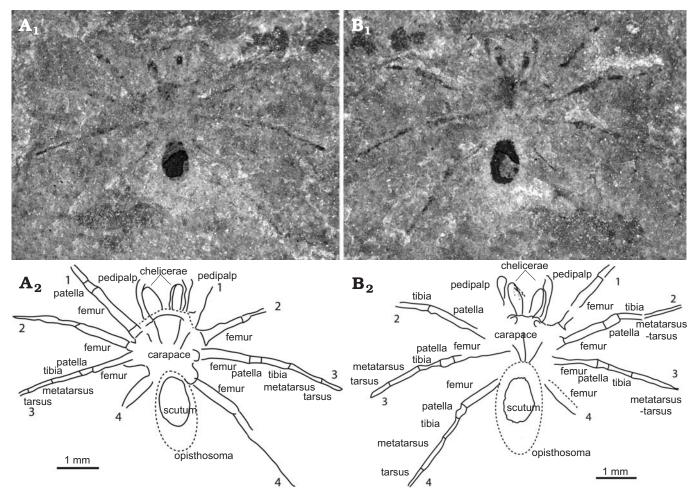
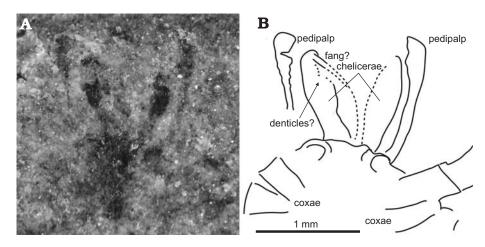


Fig. 2. Mygalomorph spider *Friularachne rigoi* gen. et sp. nov., holotype MFSN40302, Rovadia Brook valley, Friuli, Italy, late middle to early late Norian (Late Triassic); Dolomia del Forni Formation. Part (MFSN40302a) (**A**), and counterpart (MFSN40302b) (**B**). Photographs (A_1 , B_1) and explanatory drawings (A_2 , B_2). 1–4, walking legs 1–4.



oval scutum, length 1.17 mm, width 0.74 mm (L/W ratio 1.59), anteriorly positioned on opisthosoma, and extending more than half its length.

Remarks.—Distinctive features of the fossil spider which might aid identification are: large, porrect chelicerae, subequal leg lengths, and probable dorsal opisthosomal scutum. Few spiders have chelicerae nearly as long as the carapace, and these include the archaeids and related families, tetragnathids, some desids, gallieniellids, and atypoids. Of these, the third leg is much shorter than the others in the web-weaving families Tetragnathidae and Archaeidae, so the other three families are more likely candidates.

Gallieniellidae is a small family of 11 genera and 57 species (Platnick 2011) of southern-hemisphere ground spiders which commonly occur among ants. They have no fossil record. There are no fossil ants earlier than the Cretaceous, so if the association with ants is obligate, then gallieniellids would not be expected in strata as old as the Triassic. The same reasoning holds for a number of other myrmecomorphous spiders with enlarged chelicerae, e.g. salticids, corinnids, and zodariine zodariids, the last of which have enlarged chelicerae, opisthosomal scuta, and are obligate ant feeders (Jocqué 1991). Gallieniellids are thought to be plesiomorphic among gnaphosoids (Platnick 1984), but the fossil differs from gallieniellids in their lack of a dorsal opisthosomal scutum.

Desid genera which have large, porrect chelicerae are *Desis*, *Matachia*, and *Notomatachia* in both sexes, and in the males of the subfamily Myroninae (Jocqué and Dippenaar-Schoeman 2007). Some desids live in intertidal habitats, which could make them more susceptible to fossilization in marine habitats than terrestrial forms. However, desids do not bear a dorsal opisthosomal scutum.

When Millot (1947) described the first gallieniellid, *Gallieniella mygaloides*, he was struck by the similarity between the new species and mygalomorphs, as the specific epithet attests. The superfamily Atypoidea consists of three families: Atypidae, Antrodiaetidae, and Mecicobothriidae. The inclusion of Mecicobothriidae in Atypoidea has been controversial, but molecular systematic analyses have shown strong support for this composition of the superfamily (see Ayoub et al. 2007, and references therein). Males in the atypoid families Atypidae and Antrodiaetidae have extremely elongated chelicerae, similar to those Millot found in *Gallieniella*. In addition, atypid and antrodiaetid males have slen-

Fig. 3. Mygalomorph spider *Friularachne rigoi* gen. et sp. nov., holotype counterpart MFSN 40302b, Rovadia Brook valley, Friuli, Italy, late middle to early late Norian (Late Triassic); Dolomia del Forni Formation. Photograph (**A**) and explanatory drawing (**B**) of anterior part of prosoma showing anterior border of carapace, chelicerae and pedipalps.

der legs with inconspicuous setation, and they bear a dorsal scutum on the anterior part of the opisthosoma. For these reasons, the fossil is considered likely to belong to the Atypoidea.

Most atypoid males bear one or more dorsal tergites anterodorsally on the opisthosoma; see e.g., Coyle (1971: figs. 109-113, 1975: figs. 45-48; Antrodiaetidae), Kaston (1978: figs. 150, 154, 156, 158), Gertsch and Platnick (1979; Mecicobothriidae), Jocqué and Dippenaar-Schoeman (2007: figs. 12a, 18a, 58a). A single scutum, when present, is generally rather short, but a few atypids bear relatively large, single scuta, such Atypus suthepicus and A. dorsualis, both from northern Thailand and adjacent parts of Myanmar (Schwendinger 1989), several Atypus species from Korea (Namkung 2003; Kim et al. 2006), and the mainly European A. piceus (Sauer and Wunderlich 1997: 31). In some of these, the scutum bears a distinct tergite within, which is a different arrangement from that seen in the fossil. The habitus of the fossil resembles that of the atypid Calommata (e.g., Jocqué and Dippenaar-Schoeman 2007: fig. 18a) more than other atypoid genera. Nevertheless, it would be unwise to attempt to assign the fossil to an extant family with such poor preservation of details.

Geographic and stratigraphic distribution.—Type locality and horizon only.

Discussion and conclusions

Few fossil atypoids are known. Eoatypus woodwardii McCook, 1888, from the Eocene of the Isle of Wight, England, was originally described as an atypid but was placed in Opisthothelae incertae sedis by Selden (2001). Three juvenile specimens from Eocene Baltic amber were described as three new species in a new genus Balticatypus by Wunderlich (2011). An adult female atypid, Ambiortiphagus ponomarenkoi, a male antrodiaetid, Cretacattyma raveni, and a subadult male mecicobothriid, Cretomegahexura platnicki, were described from the Lower Cretaceous (?Albian, 100-112 Ma) of Mongolia by Eskov and Zonshtein (1990). These authors also described a male mecicobothriid, Cretohexura coylei, from the Lower Cretaceous (age disputed) of Transbaikalia. Wunderlich (2011) doubted the placement of Ambiortiphagus in Atypidae, on the basis of the chelicerae being somewhat shorter than in atypid males, and suggested it may lie closer to the antrodiaetids; either way, it is an atypoid.

BRIEF REPORT

In the Recent fauna, three genera of atypids, Atypus, Calommata, and Sphodros; two genera of antrodiaetids, Aliatypus and Antrodiaetus; and four genera of mecicobothriids, Hexura, Hexurella, Mecicobothrium, and Megahexura, are known (Platnick 2011). Atypus is widespread across the Palaearctic and the Far East, Calommata is an African and East Asian genus, and Sphodros is North American; all antrodiaetids are North American, except for two species of Antrodiaetus, which live in Japan; and all mecicobothrium, which occurs in Argentina, Brazil, and Uruguay (Platnick 2011).

The mygalomorph fossil record extends back to the Anisian (Middle Triassic) in the form of a hexathelid from France (Selden and Gall 1992). The atypoids are considered to be an ancient branch of the Mygalomorphae, based on both morphological and molecular phylogenetic analyses; the family lies basally in the suborder, sister to other mygalomorphs (Raven 1985; Goloboff 1993; Hedin and Bond 2006; Ayoub et al. 2007). The discovery of an atypoid of Triassic age thus concurs with these hypotheses.

Pocock (1903) discussed the geographical distribution of the Mygalomorphae, in the belief that the palaeobiogeographic history of the Mygalomorphae, which at that time were known from only Cenozoic strata, could be deduced from a consideration of their present-day distributions, especially since mygalomorphs were most unlikely to be able to disperse over great distances through ballooning, a behaviour known to occur in many araneomorphs. However, at that time, the concept of continental drift was not widely established, and Pocock (1903) explained the Palaearctic–Nearctic–Afrotropical distribution of the Atypoidea on land dispersal across Beringia during Tertiary times, followed by retreat from northern regions during the Pleistocene glaciations. The discovery of an atypoid on the shores of Tethys in Late Triassic times provides the possibility of a more widespread distribution of the superfamily across Pangaea at that time.

Modern atypids construct tubular webs in which part is buried in the substrate and the remainder lies outside, often resembling a twig. In Atypus, the external portion lies along the ground, commonly soil-covered and resembling an old-style purse (hence "purse-web"); in Sphodros, the buried part is often at the foot of a tree, and the external portion looks like an upright twig lying on the bole; the external portion of the web in *Calommata* is a small, soil-covered chamber (Fourie et al. 2011). Prey landing on the external portion is detected by the spider which then spears it through the web with the long fangs, while gripping the web from the inside. Antrodiaetids live in silk-lined burrows, which may bear a turret or collapsible collar, or be closed with a silken curtain (Gertsch 1949; Kaston 1978; Coyle and Icenogle 1994). Mecicobothriids weave a funnel-and-sheet web (Costa and Pérez-Miles 1998), similar to those made by diplurids. In atypoids, juveniles are reared initially in the web and then disperse to a suitable habitat, usually in the near vicinity. Females then live the rest of their lives inside the same web, while males, after reaching adulthood, leave the web and wander in search of females (Enock 1885). It is not surprising, therefore, that the fossil described here is an adult male, which is far more likely to be swept into a marine depositional setting than a juvenile or adult female, assuming it had a similar mode of life as modern atypoids.

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References

- Arduini, P. 1992. Clausocaris pinnai n. sp. (order Clausocarida nov.), thylacocephalan crustacean from the Norian of the Preone valley (Udine, N. Italy) and morphological consideration on Thylacocephala. Atti Società Italiana di Scienze Naturali–Museo Civico di Storia Naturale di Milano 132 (for 1991): 265–272.
- Ayoub, N.A., Garb, J.E., Hedin, M., and Hayashi, C.Y. 2007. Utility of the nuclear protein-coding gene, elongation factor-1 gamma $(EF-1\gamma)$, for spider systematics, emphasizing family level relationships of tarantulas and their kin (Araneae: Mygalomorphae). *Molecular Phylogenetics and Evolution* 42: 394–409.
- Carulli, G.B., Longo Salvador, G., Ponton, M., and Podda, F. 1997. La Dolomia di Forni: evoluzione di un bacino euxinico tardo-triassico nelle Prealpi Carniche. *Bollettino della Società Geologica Italiana* 116: 95–107.
- Carulli, G.B., Cozzi, A., Longo Salvador, G., Pernancic, E., Podda, F., and Ponton, M. 2000. Geologia delle Prealpi Carniche. *Monographs of the Museo Friulano di Storia Naturale* 44: 1–47.
- Clerck, C. 1757. Svenska spindlar, uti sina hufvud-slagter indelte samt under nagra och sextio sarskildte arter beskrefne och med illuminerade figurer uplyste. 154 pp. L. Salvii, Stockholm, Sweden.
- Costa, F.G. and Pérez-Miles, F. 1998. Behavior, life cycle and webs of Mecicobothrium thorelli (Araneae, Mygalomorphae, Mecicobothriidae). Journal of Arachnology 26: 317–329.
- Coyle, F.A. 1971. Systematics and natural history of the mygalomorph spider genus Antrodiaetus and related genera (Araneae: Antrodiaetidae). Bulletin of the Museum of Comparative Zoology, Harvard University 141: 269–402.
- Coyle, F.A. 1975. Systematics of the trapdoor spider genus *Aliatypus* (Araneae: Antrodiaetidae). *Psyche* 81: 431–500.
- Coyle, F.A. and Icenogle, W.R. 1994. Natural history of the Californian trapdoor spider genus *Aliatypus* (Araneae, Antrodiaetidae). *Journal of Arachnology* 22: 225–255.
- Cozzi, A. 2000. Il sistema norico piattaforma-bacino del M. Pramaggiore. In: G.B. Carulli (ed.), Guida alle escursioni, 80° Riunione Estiva della Società Geologica Italiana, 166–179. Edizioni Università di Trieste, Trieste.
- Dalla Vecchia, F.M. 2000. A wing phalanx of a large basal pterosaur (Diapsida, Pterosauria) from the Norian (Late Triassic) of NE Italy. *Bollettino della Società Paleontologica Italiana* 39: 229–234.
- Dalla Vecchia, F.M. 2002. Terrestrial reptiles in the Norian of the Carnian Pre-Alps (Friuli, NE Italy): paleoenvironmental implications. *Memorie della Società Geologica Italiana* 57: 101–106.
- Dalla Vecchia, F.M. 2006. The tetrapod fossil record from the Norian– Rhaetian of Friuli (northeastern Italy). *In*: J. Harris, S.G. Lucas, J.A. Spielmann, M.G. Lockley, A.R.C. Milner, and J.I. Kirkland(eds.), The Triassic–Jurassic Terrestrial Transition. *New Mexico Museum of Natural History and Science Bulletin* 37: 432–444.
- Dalla Vecchia, F.M. 2008. Vertebrati fossili del Friuli–450 milioni di anni di evoluzione. *Monographs of the Museo Friulano di Storia Naturale* 50: 1–304.
- Dalla Vecchia, F.M. 2009a. Anatomy and systematics of the pterosaur Carniadactylus gen. n. rosenfeldi (Dalla Vecchia, 1995). Rivista Italiana di Paleontologia e Stratigrafia 115: 159–186.
- Dalla Vecchia, F.M. 2009b. The first Italian specimen of the pterosaur Austriadactylus cristatus (Diapsida, Pterosauria) from the Norian (Up-

per Triassic) of the Carnic Prealps. *Rivista Italiana di Paleontologia e Stratigrafia* 115: 291–304.

- Dalla Vecchia, F.M. 2012. Il Friuli 215 milioni di anni fa Gli straordinari fossili di Preone, finestra su di un mondo scomparso. 224 pp. Comune di Preone, Cormons.
- Dalla Vecchia, F.M. and Muscio, G. 1990. Occurrence of Thylacocephala (Arthropoda, Crustacea) from the Upper Triassic of Carnic Prealps (N.E. Italy). *Bollettino della Società Paleontologica Italiana* 29: 39–42.
- Enock, F. 1885. The life-history of Atypus piceus, Sulz. Transactions of the Entomological Society of London 1885: 389–420.
- Eskov, K.Y. and Zonstein, S. 1990. First Mesozoic mygalomorph spiders from the Lower Cretaceous of Siberia and Mongolia, with notes on the system and evolution of the infraorder Mygalomorphae (Chelicerata: Araneae). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 178: 325–368.
- Fourie, R., Haddad, C.R., and Jocqué, R. 2011. A revision of the purse-web spider genus *Calommata* Lucas, 1837 (Araneae, Atypidae) in the Afrotropical Region. *ZooKeys* 95: 1–28.
- Frisia, S. 1994. Mechanisms of complete dolomitization in a carbonate shelf: comparison between the Norian Dolomia Principale (Italy) and the Holocene of Abu Dhabi Sabkha. *Special Publications of the International Association of Sedimentologists* 21: 55–74.
- Gaetani, M., Barrier, E. et al. (33 co-authors) 2000. Map 6–Late Norian (215– 212 Ma). In: J. Dercourt, M. Gaetani, B. Vrielynck, E. Barrier, B. Biju-Duval, M.F. Brunet, J.P. Cadet, S. Crasquin, and M. Sandulescu (eds.), Atlas Peri-Tethys, Palaeogeographical Maps. CCGM/CGMW, Paris.
- Garassino, A. 2000. *Glyphea rigoi* n. sp. (Crustacea, Decapoda) della Dolomia di Forni (Norico, Triassico superiore) della Carnia (Udine, NE Italia). *Gortania* 22: 59–64.
- Garassino, A., Teruzzi, G., and Dalla Vecchia, F.M. 1996. The macruran decapod crustaceans of the Dolomia di Forni (Norian, Upper Triassic) of Carnia (Udine, NE Italy). Atti Società Italiana di Scienze Naturali–Museo Civico di Storia Naturale di Milano 136 (1995): 15–60.
- Gertsch, W.J. 1949. American Spiders. xiii + 285 pp. Van Nostrand, New York.
- Gertsch, W.J. and Platnick, N.I. 1979. A revision of the spider family Mecicobothriidae (Araneae, Mygalomorphae). *American Museum Novitates* 2687: 1–32.
- Goloboff, P.A. 1993. A reanalysis of mygalomorph spider families (Araneae). American Museum Novitates 3056: 1–32.
- Hedin, M. and Bond, J.E. 2006. Molecular phylogenetics of the spider infraorder Mygalomorphae using nuclear rRNA genes (18S and 28S): conflict and agreement with the current system of classification. *Molecular Phylogenetics and Evolution* 41: 454–471.
- Jocqué, R. 1991. A generic revision of the spider family Zodariidae (Araneae). Bulletin of the American Museum of Natural History 201: 1–160.
- Jocqué, R. and Dippenaar-Schoeman, A.S. 2007. *Spider Families of the World. 2nd Edition.* 336 pp. Musée Royal de l'Afrique Centrale, Tervuren, Belgium.
- Kaston, B.J. 1978. *How to Know the Spiders. 3rd Edition*. vii + 272 pp. Wm. C. Brown, Dubuque.
- Kim, S.-T., Kim, H.-S., Jung, M.-P., Lee, J.-H., and Namkung, J. 2006. Two new purse-web spiders of the genus *Atypus* (Araneae, Atypidae) from Korea. *Journal of Arachnology* 34: 170–175.
- Mattavelli, L. and Rizzini, A. 1974. Facies euxiniche nelle dolomie noriche dell'Ampezzano (Udine): petrografia e sedimentologia. *Memorie della Rivista Italiana di Paleontologia e Stratigrafia* 14: 111–140.
- McCook, H.C. 1888. A new fossil spider, *Eoatypus woodwardii*. Proceedings of the Academy of Natural Sciences of Philadelphia 1888: 200–202.

- Millot, J. 1947. Une araignée malgache enigmatique, Gallieniella mygaloides n. g., n. sp. Bulletin du Muséum National d'Histoire Naturelle, Paris, serie 2 19: 158–160.
- Moix, P., Kozur, H.W., Stampfli, G.M., and Mostler, H. 2007. New paleontological, biostratigrafical and paleogeographic results from the Triassic of the Mersin Mélange, SE Turkey. *In*: S.G. Lucas and J.A. Spielmann (eds.), The Global Triassic. *New Mexico Museum of Natural History Science Bulletin* 41: 282–311.
- Muttoni, G., Kent, D.V., Jadoul, F., Olsen, P.E., Rigo, M., Galli, M.T., and Nicora, A. 2010. Rhaetian magneto-biostratigraphy from the Southern Alps (Italy): Constraints on Triassic chronology. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* 285: 1–16.
- Namkung, J. 2003. *The Spiders of Korea, 2nd Edition*. 648 pp. Kyo-Hak Publishing Company, Seoul.
- Ogg, J.G., Ogg, G., and Gradstein, F.H. 2008. *The Concise Geologic Time Scale*. 177 pp. Cambridge University Press, Cambridge.
- Platnick, N.I. 1984. Studies on Malagasy spiders, 1. The family Gallieniellidae (Araneae, Gnaphosoidea). American Museum Novitates 2801: 1–17.
- Platnick, N.I. 2011. The world spider catalog, version 12.0. American Museum of Natural History, online at http://research.amnh.org/iz/spiders/ catalog.
- Pocock, R.I. 1892. Liphistius and its bearing upon the classification of spiders. Annals and Magazine of Natural History, Series 6 10: 306–314.
- Pocock, R.I. 1903. On the geographical distribution of spiders of the order Mygalomorphae. *Proceedings of the Zoological Society of London* 103: 340–368.
- Raven, R. 1985. The spider infraorder Mygalomorpha (Araneae): cladistics and systematics. *Bulletin of the American Museum of Natural History* 182: 1–180.
- Renesto, S., Dalla Vecchia, F.M., and Peters, D. 2002. Morphological evidence for bipedalism in the Late Triassic prolacertiform reptile *Langobardisaurus*. *In*: M. Gudo, M. Gutmann, and J. Scholz (eds.), Concepts of Functional Engineering and Constructional Morphology: Biomechanical Approaches on Fossil and Recent Organisms. *Senckenbergiana lethaea* (Special issue) 82: 95–106.
- Roghi, G., Mietto, P., and Dalla Vecchia, F.M. 1995. Contribution to the conodont biostratigraphy of the Dolomia di Forni (Upper Triassic, Carnia, NE Italy). *Memorie di Scienze Geologiche* 48: 125–133.
- Sauer, F. and Wunderlich, J. 1997. Die schönsten Spinnen Europas, 5th Edition. 300 pp. Fauna-Verlag, Karlsfeld.
- Schwendinger, P.J. 1989. On the genus *Atypus* (Araneae: Atypidae) in northern Thailand. *Bulletin of the British Arachnological Society* 8: 89–96.
- Scotti, P., Fantoni, R., Podda, F., and Ponton, M. 2002. Depositi norici di ambiente anossico nelle Prealpi Friulane (Italia nord-orientale). *Memorie della Società Geologica Italiana* 57: 65–78.
- Selden, P.A. 2001. Eocene spiders from the Isle of Wight with preserved respiratory structures. *Palaeontology* 44: 695–729.
- Selden, P.A. and Gall, J.-C. 1992. A Triassic mygalomorph spider from the northern Vosges, France. *Palaeontology* 35: 211–235.
- Selden, P.A., Anderson, J.M., Anderson, H.M., and Fraser, N.C. 1999. Fossil araneomorph spiders from the Triassic of South Africa and Virginia. *Journal of Arachnology* 27: 401–414.
- Selden, P.A., Anderson, H.M., and Anderson, J.M. 2009. A review of the fossil record of spiders (Araneae) with special reference to Africa, and description of a new specimen from the Triassic Molteno Formation of South Africa. *African Invertebrates* 50: 105–116.
- Thorell, T. 1870b. On European spiders. Nova Acta Regiae Societatis Scientarium Upsaliensis, Seriei Tertiae 7: 109–242.
- Wunderlich, J. 2011. Some fossil spiders (Araneae) in Eocene European ambers. *Beiträge zur Araneologie* 6: 472–538.

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