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The significance of male pedipalpal characters for the higher systematics of the crab spider genus *Xysticus* C.L. Koch, 1835 (Araneae: Thomisidae)

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Abstract
Male pedipalp characters support the hypothesis that there are potentially at least three clades within European *Xysticus* s.l. C.L. Koch, 1835 (Araneae: Thomisidae). These clades correspond with the older, but currently synonymised, genera *Proxysticus* Dalmas, 1922 and *Psammitis* Menge, 1875. Synapomorphies in the male pedipalp shared with other thomisid genera (e.g. *Coriarachne* Thorell, 1870, *Ozyptila* Simon, 1864) suggest that *Xysticus* s.l. represents a paraphyletic group.

Key words: Thomisidae, *Xysticus*, *Psammitis*, *Proxysticus*, systematics, phylogeny

INTRODUCTION

Xysticus C.L. Koch, 1835 is the most species-rich genus within the family Thomisidae (crab spiders) and contains more than 340 species (Ono 1988). These are widely distributed, but occur mainly in the northern hemisphere. It is not the number of species but the enormous heterogeneity in genital and morphological characters within the *Xysticus* species that makes it difficult to resolve relationships between them. Despite the efforts of previous authors to subdivide it (see below), the taxonomic status of this crab spider genus is uncertain and it is currently regarded as a large *Xysticus* sensu lato group (Brignoli 1983, Platnick 1997). Close investigation of middle European species suggests that structures in the male palp include apomorphic characters which may be used to define distinct groups, at least within the European *Xysticus* s.l. Furthermore, some of these apomorphic characters appear to be present in other thomisid genera and thus draw into question the monophyly of *Xysticus* s.l.

HISTORY

During the last 150 years there have already been other arachnologists who realised that *Xysticus* is heterogeneous and tried to solve the problem by splitting the genus or establishing subtaxa. Some of the main points in the history of *Xysticus*, since it was first described by C.L. Koch in 1835, are the separating by Thorell of *Coriarachne* Thorell, 1870, the separation of two new genera from *Xysticus* by Menge (*Psammitis* Menge, 1875 and *Spiracme* Menge, 1875) and the creation by Dalmas of the new genus *Proxysticus* Dalmas, 1922.

Thorell (1870) considered *Coriarachne* as a distinct genus not only because of the flattened body, but also because of the different arrangement of the eyes. Obviously impressed by the screw-like embolus and the flat tegulum without any protruding parts, Menge (1875) estab-

Table 1. Previous suggestions of subgroups and subgenera in *Xysticus* s.l.

Simon 1932: *Xysticus*, 4 subgroups	
	cristatus
	longipes
	sabulosus
	robustus
Gertsch 1939: *Xysticus*, 5 groups	
	cristatus
	cunctator
	concursus
	sabulosus
	robustus
Gertsch 1953: *Xysticus*, 2 subgenera	
	Xysticus
	Spiracme
Schick 1965: *Xysticus*, 5 subgenera	
	Pellysticus
	Lassysticus
	Xysticus
	Psammitis
	Proxysticus

lished the new genus *Spiracme*. He also stated in his diagnosis of the genus that the body is elongate and the eyes are similar to *Xysticus*, but that the lateral eyes are somewhat larger. For *Psammitis*, the second genus he established, he referred to the disk-like tegulum and the embolus surrounding it. Again he also used the different size of the lateral eyes to distinguish *Psammitis* from *Xysticus*. Dalmas (1922) described the males of his new genus *Proxysticus* as lacking any tegular apophyses, but with a protruding area in the middle of the bulb and an evenly twisted embolus.

As Ono (1988) stated, the tendency after that time was rather to establish subgroups or subgenera, (e.g. Simon 1932; Gertsch 1939, 1953; Schick 1965; see Table 1). In particular Schick (1965) intensively studied male palp characters not only of *Xysticus*, but of other nearctic thomisids too. Based on the recognition of the different types of tutacula, emboli and tegular apophyses he suggested the subgenera *Pellysticus* Schick, 1965, *Xysticus* C.L. Koch and *Lassysticus* Schick, 1965, belonging to the apophysate (i.e. apophyses present) division, and the subgenera *Proxysticus* Dalmas and *Psammitis* Menge, belonging to the anapophysate division. Later Wunderlich (1987, 1994) resurrected *Psammitis* as a distinct genus. He characterised the males of *Psammitis* by a tegulum with 1 or 2 humps/'pockets' and/or one apophysis (but never with two apophyses as in *Xysticus*), with a long or short embolus and 2-4 tibial apophyses. On the contrary he defined *Xysticus* by the presence of two tegular apophyses, never with a sickle-shaped pocket (as in *Psammitis*), two tibial apophyses and a long and thin embolus (Wunderlich, 1994, p. 751). This was not followed by other arachnologists and despite all earlier efforts in the history of *Xysticus*, the spider catalogues (Brignoli 1983, Platnick 1997) still list *Xysticus* as a single, large species-complex. For example Platnick (1997) rejected both *Proxysticus* and *Psammitis*, noting the absence of comprehensive studies and regarded *Xysticus* as a large *sensu lato* group.

MATERIALS AND METHODS

This study is based on alcohol preserved material belonging to different museum collections (e.g. Basel, Berne, Berlin, Frankfurt, Stockholm, Paris, Vienna) and to private collections. More than 30 different *Xysticus* species, all of which are found in central Europe, have been examined and the structure of the male pedipalp has been studied intensively. The species examined were: *X. acerbus* Thorell, 1872, *X. albomaculatus* Kulczyński, 1891, *X. apricus* L. Koch, 1875, *X. audax* (Schrank, 1803), *X. bifasciatus* C.L. Koch, 1837, *X. bonneti* Denis, 1938, *X. cor* Canestrini, 1873, *X. cristatus* (Clerck, 1757), *X. desidiosus* Simon, 1875, *X. embriki* Kolosvary, 1935, *X. erraticus* (Blackwall, 1834), *X. ferrugineus* Menge, 1875, *X. gallicus* Simon, 1875, *X. ibex* Simon, 1875, *X. kempeleni* Thorell, 1872, *X. kochi* Thorell, 1872, *X. lanio* C. L. Koch, 1835, *X. lineatus* (Westring, 1851), *X. luctator* L. Koch, 1870, *X. luctuosus* (Blackwall, 1836), *X. macedonicus* Šilhavý, 1944, *X. marmoratus* Thorell, 1875, *X. ninnii* Thorell, 1872, *X. obscurus* Collett, 1877, *X. paniscus* L. Koch, 1875, *X. robustus* (Hahn, 1832), *X. sabulosus* (Hahn, 1832), *X. secedens* L. Koch,

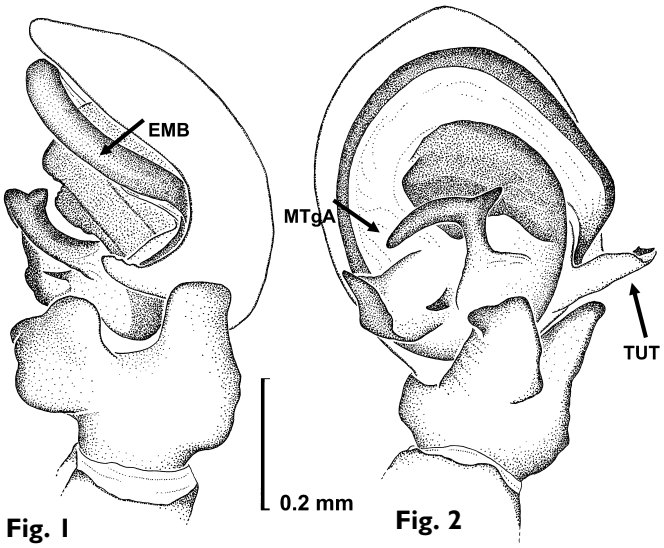

Fig. 1-2. Left pedipalp, *Xysticus cristatus* (Clerck, 1757), priv. Coll. Peter Horak (Tirol, nr. Innsbruck, 590 m, Meyer leg.) 1: retrolateral, 2: ventral. Abbreviations: EMB: embolus, MTgA: median tegular apophysis, TUT: tutaculum.

1875, *X. striatipes* L. Koch, 1870, *X. tortuosus* Simon, 1932, *X. ulmi* (Hahn, 1831), *X. viduus* Kulczyński, 1898.

The similar-looking genera *Coriarachne* and *Ozyptila* Simon, 1864 were also examined, since provisionial observations suggested that male pedipalpal characters seen in *Xysticus* are also present in these taxa. For outgroup comparison the pedipalp morphology of various thomisid genera (including the species *Misumena vatia* (Clerck, 1757), *Misumenops tricuspidatus* (Fabricius, 1775), *Synaema globosum* (Fabricius, 1775), *Coriarachne depressa* (C.L. Koch, 1837), *Coriarachne fulvipes* (Karsch, 1879), *Ozyptila trux* (Blackwall, 18469 and *Thomisus onustus* Walckenaer, 1806), was studied from the literature (e.g. Ono 1988; Roberts 1995) or from specimens deposited at the Museum für Naturkunde, Berlin, and my own private collection.

RESULTS

My studies on central European representatives of *Xysticus* s.l. suggest that there exist at least three different groups within Europe, which can potentially be diagnosed on autapomorphies derived from the male pedipalp (Table 2).

In *Xysticus* the pedipalp is usually characterised by the presence of tibial apophyses (mostly ventral and retrolateral tibial apophyses, sometimes intermediate tibial apophysis – respectively VTiA, RTiA, ITiA) and tegular apophyses with various forms and shapes from hook-like structures to simple ridges. A tutaculum is present at the retrolateral edge of the bulbus. Its size and shape are variable.

Group 1 - '*Xysticus* sensu stricto' (Figs. 1, 2)
Xysticus cristatus (Clerck, 1757) is a common representative of this group, which can be defined by a very complex tegular structure with at least two distinct tegular apophyses. The embolus is elongate, whip-like and its tip lies within a simply constructed tutaculum (Fig. 2). The tibia bears two apophyses (VTiA, RTiA). *Xysticus audax,* the type species of the genus *Xysticus*, also belongs here, being part of the *cristatus* group (e.g. Jantscher 2001).

Group 2 - '*Proxysticus*' (Figs. 3, 4)
The drawings show the pedipalp of *Xysticus robustus* (Hahn, 1831). This group also has a long embolus originating at the basal part of the bulb. Again the tutaculum is simply built, but the tegulum is different. It does not carry distinct apophyses but is merely slightly structured in the centre. Three apophyses (VTiA,

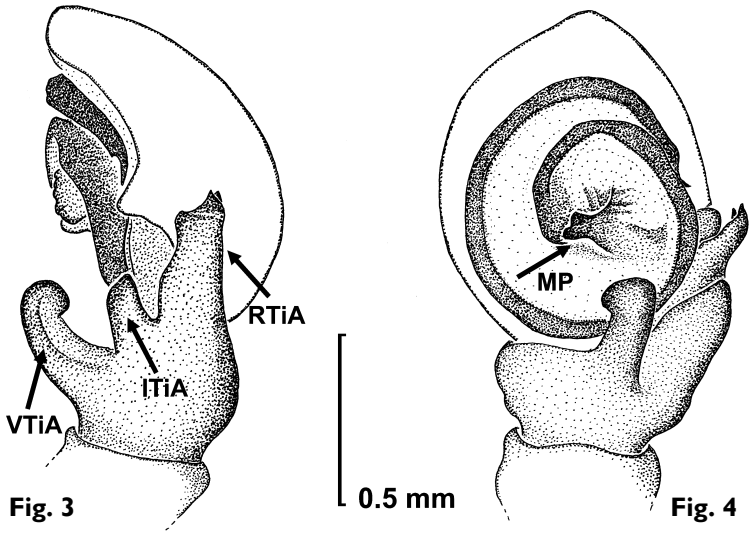

Fig. 3-4. Left pedipalp, *Xysticus robustus* (Hahn, 1831), Natural History Museum Basel 438c, 3: retrolateral, 4: ventral. Abbreviations: ITiA: intermediate tibial apophysis, MP: median projection, RTiA: retrolateral tibial apophysis, VTiA: ventral tibial apophysis.

ITiA and RTiA) are present on the tibia, each emerging from its own base.

Group 3 - '*Psammitis*' (Figs. 5, 6)
This group, represented here by *Xysticus sabulosus* (Hahn, 1831), is characterised by the completely flat tegulum without any special structures but at best simple ridges. The embolus originating at the apical part of the bulbus is, in comparison to those of the other groups, very short and often characteristically shaped (e.g. screw-like). In cases where the embolus is

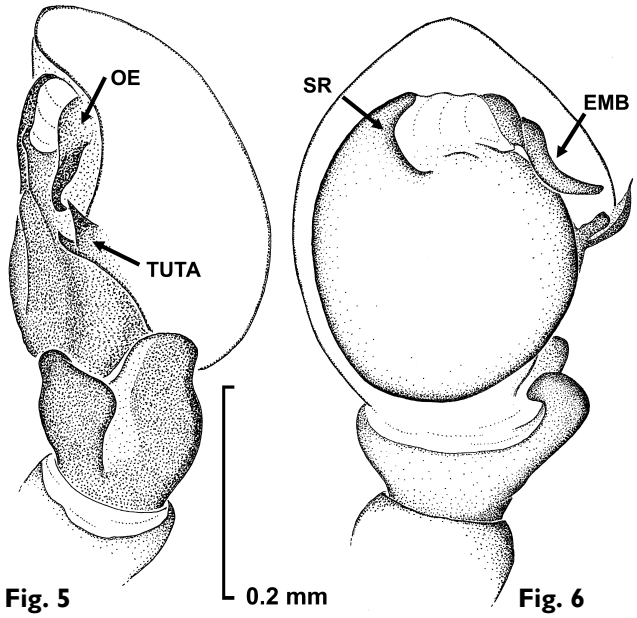

Fig. 5-6. Left pedipalp, *Xysticus sabulosus* (Hahn, 1831), Natural History Museum Basel 1894d, 5: retrolateral, 6: ventral. Abbreviations: EMB: embolus, OE: origin of embolus, SR: sclerotised ridge, TUTA: tutacular apophysis.

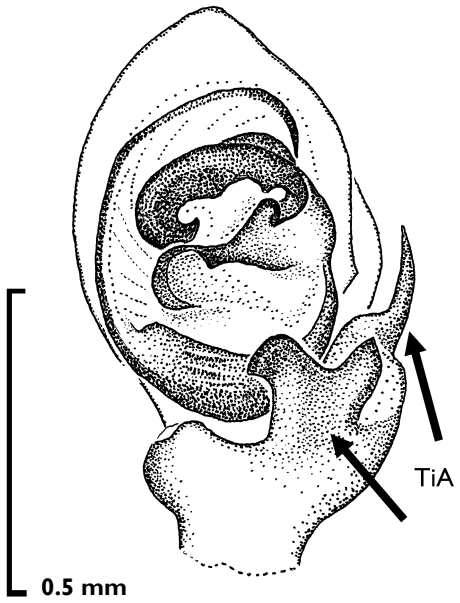

Fig. 7. Left pedipalp, *Ozyptila trux* (Blackwall, 1846), after Roberts (1995, p. 167), ventral. Abbreviations: TiA = tibial apophyses

twisted, it can reach a considerable length, but always originates in the apical area of the bulbus. In most cases the terminal part of the embolus does not reach the tutaculum. Surprisingly, this structure is more complex than in the other two groups and often even two pointed tips (tutaculum and tutacular apophysis) are present instead of one simple structure. The tibia bears the usual ventral and retrolateral apophyses.

Ozyptila (Fig. 7)
This genus, here represented by *Ozyptila trux* (Blackwall, 1846), has a structured tegulum with more or less distinct apophyses. The tibial apophyses are highly complex and do not fit clearly into the VTiA-RTiA scheme but possibly the VTiA and RTiA share a common base.

Coriarachne (Figs. 8-9)
The drawings show *Coriarachne fulvipes* (Karsch, 1879). *Coriarachne* is characterised by a very flat tegulum without any apophyses but simply a sickle-shaped ridge in the upper part of the bulb. Two tibial apophyses (VTiA, RTiA) are present. The tutaculum is small and far away from the embolus tip. The embolus is short and originates in the apical area of the bulb. Note that the overall shape is very similar to *'Psammitis*.*

To date there is no published cladogram of the Thomisidae at the genus level, thus the sister

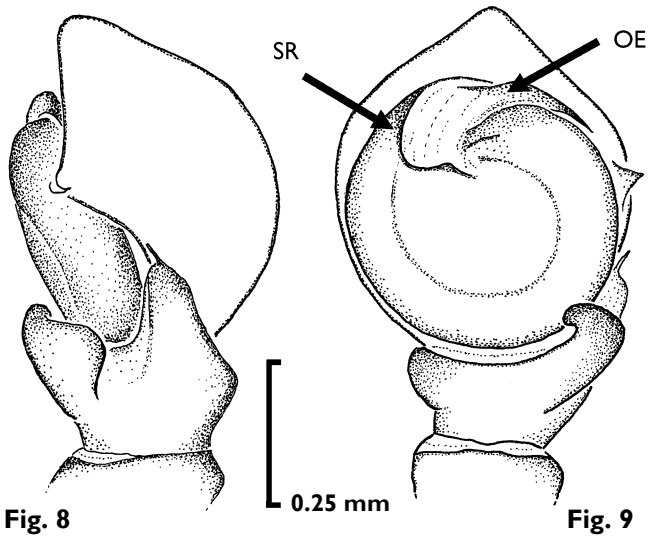

Fig. 8 Fig. 9

Fig. 8-9. Left pedipalp, *Coriarachne fulvipes* (Karsch, 1879), after Ono (1988, figs. 60-61), 8: retrolateral, 9: ventral. Abbreviations: OE: origin of embolus, SR: sclerotised ridge.

Table 2. Autapomorphies for the groups identified here and the related genera

'Xysticus s.s.':	two or more distinct bulbar apophyses
'Psammitis':	modified tutaculum
'Proxysticus':	three tibial apophyses
Ozyptila:	small size, modified body spination
Coriarachne:	flat body

group of *Xysticus* s.l. remains to be determined. However, a flattened tegulum occurs widely in other thomisid genera (see e.g. figs. in Roberts 1995) such as *Thomisus* Walckenaer, 1805, *Synaema* Simon, 1864, *Misumenops* F.O.P.-Cambridge, 1900, *Pistius* Simon, 1875, *Heriaeus* Simon, 1875, *Misumena* Latreille, 1804 and *Runcinia* Simon, 1875 and is therefore potentially plesiomorphic for *Xysticus*.

The plesiomorphic number of tibial apophyses is more difficult to polarise but two simple apophyses occur in a number of thomisid genera, e.g. *Thomisus, Synaema, Runcinia.* This character state may therefore be plesiomorphic for Thomisidae, but in other genera there are clearly three distinct apophyses (see '*Proxysticus*', Fig. 3) or complex combinations in which the apophyses seem to fuse with one another (see *Ozyptila*, Fig. 7). These modifications are potential apomorphies compared to the simple morphology noted above.

A short summary of the autapomorphies for these probably monophyletic *Xysticus* groups, as well as for the related genera *Ozyptil*a and *Coriarachne*, is given in Table 2.

DISCUSSION

A significant result of this study is that it was not possible to find an obvious autapomorphy in the pedipalp to support the monophyly of the currently accepted *Xysticus* s.l. group. By contrast, possible clades within *Xysticus* s.l. have been identified, based on distinct, apomorphic male genital characters: *'Psammitis', 'Xysticus* sensu stricto*'* and *'Proxysticus'* (Table 2). Whether these palpal characters justify resurrecting *Psammitis* and *Proxysticus* is unclear at present, but the names remain available. Currently I consider Menge´s genus *Spiracme* as a possible synonym of '*Psammitis'* although the type of the female epigyne does not match with those of other representatives of *'Psammitis*'. Furthermore, these clades potentially share synapomorphies in the pedipalp with other thomisid genera, i.e. *Coriarachne* and *Ozyptila* in this study. This supports the hypothesis that *Xysticus* s.l. is a paraphyletic assemblage of common crab spiders.

One provisional clade is (*Coriarachne* + '*Psammitis*') the synapomorphy for which could be the modified embolus originating in the apical part of the bulbus (Figs. 5-6, 8-9, OE), although this character must be tested against other taxa. There are further thomisid genera where the tegulum and embolus also show remarkable similarities to the (*Coriarachne* + '*Psammitis*') synapomorphy suggested here, e.g. *Misumena*, *Pistius*, and these could belong to this group too. The second provisional clade is (*'Xysticus* s.s.*'* (*'Proxysticus'* + *Ozyptila*)). This entire clade is defined by the structured tegulum (Figs. 2, 4, 7), as opposed to the plesiomorphic flat tegulum (Figs. 6, 9). The synapomorphy of (*'Proxysticus'* + *Ozyptila*) is the presence of complex tibial apophyses. '*Proxysticus*' is characterised by three tibial apophyses and *Ozyptila* also shows a highly complex tibia (Fig. 8), but the apophyses do not each emerge from a distinct and separate base. So far it is not clear which parts are homologous to the different apophyses. Both these clades, if correct, imply that *Xysticus* s.l. is not a monophyletic group.

Female genital characters, which are very complex and need to be studied in more detail, also support the hypothesis of three groups within *Xysticus* s.l. Corresponding with the three potential groups, three types of epigynes can be found, but these characters are not com-

prehensively discussed here. However, included here is a brief survey of the three major types of epigynes. In the *'Xysticus* s.s.*'* group the epigyne is usually characterised by the presence of one or two deep depressions, the genital atria. In the latter case the atria are separated from each other by a distinct median septum, e.g. in *Xysticus cristatus* (e.g. Roberts 1985, text fig. 39a). *'Psammitis'* on the contrary merely shows one slight depression mostly in combination with a groove (e.g. Roberts 1985, text fig. 40d). The genital opening is not so obvious as it is in *Xysticus* s.s. Females of *'Proxysticus'* have a highly characteristic epigyne: heavily sclerotised large bulges and folds surrounding a pocket-like structure in the middle of the epigynal plate (e.g. Roberts 1985, text fig. 41b).

Other characters in *Xysticus*, like body shape or spination, should also be closely investigated and could contribute further characters. These provisional results must also be tested against non-European material, in which other potential subgroups might be expected.

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