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Fossil scorpions from the Buntsandstein (Early Triassic) of France

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Abstract

Two new families, genera, and species of fossil scorpion are described from the Buntsandstein (Early Triassic) of France, the Voltzia Sandstone Formation. They give evidence for the recovery of terrestrial ecosystems severely reduced during the Late Permian mass extinction. One of these fossil families can be classified together with extant families within the Buthoidea (sensu Lourenço). This suggests that these modern scorpions belong to lineages present at least for 200 Myr. The second fossil family, tentatively placed in the superfamily Mesophonoidea Wills, exhibits several features inherited from Palaeozoic lineages. ***To cite this article: W.R. Lourenço, J.-C. Gall, C. R. Palevol 3 (2004)***.

Résumé

Scorpions fossiles du Buntsandstein (Trias inférieur) de France. Deux nouvelles espèces de scorpions rapportées à deux nouvelles familles sont décrites. Elles proviennent de la formation du Grès à Voltzia de l'Est de la France (Buntsandstein, Trias inférieur) et illustrent la restauration de la biodiversité après sa dramatique extinction de la fin du Permien. Un des nouveaux taxons peut être classé dans la super-famille actuelle des Buthoidea (sensu Lourenço), une lignée dont l'existence serait ainsi attestée depuis au moins 200 Ma. En revanche, la deuxième famille, provisoirement placée dans la super-famille des Mesophonoidea Wills, présente encore plusieurs caractères hérités des formes paléozoïques. L'abondance des scorpions dans les gisements fossilifères du Buntsandstein des Vosges met en évidence la place prépondérante qu'ils occupaient à l'époque dans la région, dans le monde des petits prédateurs. ***Pour citer cet article : W.R. Lourenço, J.-C. Gall, C. R. Palevol 3 (2004)***.

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Mots clés : Scorpion ; Fossile ; Crise biologique ; Prédateur ; Trias inférieur ; Buntsandstein ; France

Version française abrégée

Les scorpions fossiles du Mésozoïque sont rares. Seules quelques formes isolées du Trias et du Jurassique sont citées dans la littérature [19]. Leur présence au Crétacé a été confirmée par des découvertes récentes [1,13–15].

Dans les gisements fossilifères du Grès à Voltzia des Vosges du Nord, datés du Buntsandstein supérieur (Trias inférieur), plusieurs centaines d'échantillons de scorpions fossiles ont été collectés. Ils autorisent une diagnose précise de deux nouvelles espèces, attribuées à deux genres nouveaux et à deux familles nouvelles. Leurs affinités taxonomiques ont pu être précisées, ainsi que leurs relations phylogénétiques avec des groupes modernes et paléozoïques.

Deux nouvelles familles sont proposées : les Protobuthidae fam. n. et les Gallioscorpionidae fam. n. Leurs diagnoses sont les suivantes.

Protobuthidae. Scorpions de taille moyenne à petite; adultes avec environ 32/33 mm de longueur totale. Corps et appendices très élancés ; pédipalpes avec 18,9 et 19,2 mm de longueur. Tubercule oculaire situé légèrement en avant de la plaque prosomienne. Anneaux du metasoma avec 10–8–8–8–5 carènes. Vésicule avec une forme ovale ; aiguillon plus long que la vésicule ; épine sous-aiguillonnaire absente. Trichobothriotaxie très incomplète, mais rappelant un type A « basique ». Trois à quatre trichobothries ont été observées sur les faces dorsale/externe de la pince ; 2–3 sur le doigt fixe ; 3–4 dorsales sur le tibia ; 2 dorsales et 1–2 externes sur le fémur. Tranchant du doigt fixe, probablement composé d'une seule série linéaire de granules.

Gallioscorpionidae. Scorpions de taille moyenne; adultes avec environ 50 à 60 mm de longueur totale. Corps et appendices moyennement élancés. Carapace toujours plus large que longue. Tubercule oculaire situé dans la partie antérieure de la carapace, sur une zone protubérante ; yeux de grande taille, séparés par moins d'un diamètre oculaire ; yeux latéraux également situés sur une zone protubérante, et constitués de plusieurs ocelles, mais pas composés. Sternum pentagonal, trois fois plus long que large. Stigmates très réduits, avec une forme entre linéaire et ovale. Peignes de grande taille, avec 31 à 38 dents et la présence de fulcres. Telson de forme arrondie; aiguillon très long et épine sous-aiguillonnaire absente. Modèle trichobothrial d'un type A « basique ». Deux trichobothries ont été observées sur les faces dorsale/externe de la pince, 2 sur le doigt fixe, 3 dorsales et une interne sur le tibia ; 2 dorsales, 1 externe et 1 interne sur le fémur. Tranchant du doigt fixe probablement composé d'une seule série linéaire de granules. Eperons basitarsaux présents sur les pattes III et IV ; tibiaux sur les pattes IV.

L'abondance des scorpions dans les sites fossilifères du Buntsandstein confirme la position prépondérante qu'occupaient ces arthropodes parmi les prédateurs des terres émergées du Trias. Leurs proies provenaient d'une riche entomofaune. Contemporains de la restauration de la biosphère après sa dramatique décimation à la fin du Permien, les scorpions du Buntsandstein révèlent la coexistence, dans les mêmes biotopes, de deux espèces. Chez l'une, *Gallioscorpio*, les affinités avec les formes paléozoïques sont encore évidentes. En revanche, le genre *Protobuthus* peut être classé, grâce à de nombreux caractères, dans la famille crétacée des Archaeobuthidae, mais aussi dans la famille actuelle des Buthidae, au sein des Buthoidea. Son existence prouve que des scorpions modernes peuvent être reliés à des lignées déjà présentes depuis au moins 240 Ma. À l'exemple des crustacés et des insectes du Buntsandstein, les scorpions attestent que, après la crise biologique du Permien, le remplacement des biocénoses fut progressif. Les milieux de transition, à l'instar de l'environnement deltaïque du Grès à Voltzia, se révèlent des sites privilégiés, à la fois pour la persistance de formes héritées du Paléozoïque et pour l'émergence des faunes modernes.

1. Introduction

On account of the lack of mineralised cuticles and their mainly terrestrial habitats, scorpions are scarce in the palaeontological record. Although listed since the Palaeozoic, only a few cases are known from the Triassic, Jurassic and Cretaceous periods. Sissom [19] reports five known occurrences during the Triassic and two in the Jurassic. Only recently have some discoveries confirmed the presence of scorpion fossils for the Cretaceous period [1,13–15]. The Fossil-Lagerstätten of the Upper Buntsandstein of northeastern France, the 'Grès à Voltzia' Formation, fortunately fill a gap in the record of the palaeontological history of scorpions. Particularly favourable circumstances have preserved non-mineralised soft tissues such as the chitin of arthropod cuticles from both terrestrial and aquatic faunas [4]. The Grauvogel and Gall collection is the result of tens of years prospecting in the 'Grès à Voltzia' localities. It contains several hundreds scorpion specimens, including some entire individuals. In account of their Anisian age, these fossils are older than those described by Wills [23,24] from the Triassic of Great Britain. Accurate diagnoses are proposed for the new families, genera and species described in this paper.

2. Geological framework

The 'Grès à Voltzia' correlates with the upper part of the Buntsandstein. It covers the passage of time between the fluviatile Lower Triassic red beds and the transgressive marine sedimentation of the Middle Triassic [5]. Its lower unit, or 'Grès à meules', is about 20 m thick and exhibits the typical facies interfingering of the subaerial part of a deltaic environment. The fossiliferous horizons are located in lenses of green or red shales that were deposited in temporary pools of water formed in abandoned channels or in depressions of the flood plain. The fossils are excellently preserved. They belong to aquatic animals (medusids, annelids, lingulids, bivalves, limulids, crustaceans, insect larvae, fishes) as well as to terrestrial animals (spiders, scorpions, myriapods, insects, reptile footprints) and to an abundant flora (ferns, horsetails, conifers). The vegetation grew on the margins of the channels and in standing bodies of water [6] that were also inhabited by numerous terrestrial arthropods. The scorpions lived in company with a varied entomological fauna comprising more than 200 species of insects (cockroaches, mayflies, beetles, bugs... [16]). The climate was semi-arid. During long dry seasons, the pools became isolated and dried out. From time to time, torrential rains generated floods that suddenly dropped the coarser sandy material downstream.

3. Taxonomic treatment

Since the major revision of Kjellesvig-Waering [10], summarized by Sissom [19], only a few additions to the known Palaeozoic fossils have been made, mainly by Jeram [7–9]. Like Selden [17], this author adopted a scheme that followed the classification of Stockwell – unpublished PhD dissertation [20]. This treats scorpions as a class Scorpionida, with three orders: Protoscorpiones, Palaeoscorpiones, and Scorpiones. In their catalogue of the scorpions of the world, Fet et al. [3] insist on the complicate task of dealing with the analysis and classification of scorpions at the class/order group levels, since the Code does not regulate names above the rank of family. They retain the system of Kjellesvig-Waering [10] – with the family-group synonymies introduced later – as the only existing comprehensive system, but realize that future reanalysis will almost certainly result in significant changes.

Superfamily Buthoidea C.L. Koch, 1837 (*sensu* Lourenço)

Protobuthidae new family

With the exception of some Cretaceous fossils [1,13–15], previously described Mesozoic scorpion fossils from Jurassic and Triassic have not been assigned to any extant superfamily [19]. Careful analysis of several characters, and in particular of the trichobothrial pattern presented by this fossil element, led us to conclude that the new material described here can actually be placed in the superfamily Buthoidea *sensu* Lourenço [12]. This fossil family Protobuthidae shows some affinities with the Cretaceous fossil family Archaeobuthidae Lourenço, 2001 and with modern family Buthidae C.L. Koch, 1837. Several characters are, however, divergent, and the fossil scorpions appear to be more like a proto-element *(sedis mutabilis)* of these two families.

Diagnosis. Scorpions of medium to small size (32.5 mm in total length). Very slender body and ap-

pendages; pedipalps 18.9 and 19.2 mm in length. Median ocular tubercle only slightly anterior to the centre of the carapace; median eyes large and separated by less than one ocular diameter (see paratype). Metasomal segments: I with 10 carinae; II–IV with 8 carinae; V with 5 carinae. Telson: vesicle with an oval shape; aculeus slender and longer than the vesicle (see Table 1); subaculear tooth absent. Trichobothrial pattern very incomplete but recalling the 'basic' type A [21]. The following trichobothria can be observed: 3–4 dorso-external on chela manus; 2–3 in the fixed finger; 3–4 dorsal on patella; 2 dorsal and 1–2 external

Table 1
Morphometric values (mm) of the male holotype and juvenile paratype of *Protobuthus elegans* sp. n. and of the holotype of *Gallioscorpio voltzi* sp. n

	Protobuthus elegans	*Gallioscorpio voltzi* sp. n.	
	Male holotype	Juvenile paratype	Holotype
Total length	32.5	9.3	60.1
Carapace:			
– length	3.5	1.2	5.8
– anterior width	2.5	—	6.8
– posterior width	3.9	—	8.3
Mesosoma length	14.1	4.2	24.0
Metasomal length	14.9	3.9	30.3
Segment I:			
– length	2.3	4.0	
– width	—	—	6.0
– depth	1.3	—	
Segment II:			
– length	2.9	—	6.2
– width	—	—	6.1
– depth	1.2	—	—
Segment III:			
– length	3.1	—	6.3
– width	—	—	6.0
– depth	1.4	—	—
Segment IV:			
– length	3.2	—	6.6
– width	—	—	6.0
– depth	1.4	—	—
Segment V:			
– length	3.4	—	7.2
– width	—	—	6.0
– depth	1.4	—	
Vesicle:			
– length	2.4	—	—
– depth	1.1	—	—
Aculeus length	2.5	—	—
Pedipalp:	R/L		
– femur length	4.7/4.9	—	8.4
– femur width	1.0/1.0	—	2.2
– patella length	5.1/5.0	—	8.6
– patella width	1.6/1.4	—	3.4
– chela length	9.1/9.3	—	14.8
– chela width	1.3/1.4	—	2.6
Movable finger:			
– length	6.3/6.2	—	12.2

on the femur. Dentate margins of fixed finger probably composed of a single linear row of granules. Legs: tibial spurs not observable.

Type of the new family: genus ***Protobuthus*** new genus.

Type species: Protobuthus elegans sp. n.

Diagnosis: the same as for the new family.

Protobuthus elegans sp. n. (Figs. 1, 2, 10–12).

Type material. Holotype: 7899 (A–B); possibly an adult or pre-adult male, in part and counterpart. Paratype: 7907 (A-B); juvenile individual in part and counterpart. From France, Vosges, Voltzia Sandstone Formation, Bust (collection Grauvogel & Gall). Depositary: 'Laboratoire de paléontologie, université Louis-Pasteur', Strasbourg , France.

Etymology. The specific name makes reference to the slender body and appendages of this species.

Morphology.

- Prosoma: Anterior margin weakly emarginated, almost straight. No furrows can be observed clearly. Tegument rather smooth. Median ocular tubercle only slightly anterior to the centre of the carapace (see paratype); median eyes separated by less than one ocular diameter. Three or four pairs of lateral eyes can be observed with difficulty.
- Mesosoma: Tergites I-VI with median carina moderate to weak. Tergite VII pentacarinate, with lateral pairs of weak carinae. Intercarinal spaces weakly granular, almost smooth. Sternites not observable. Pectines not observable. Metasoma: Segment I with 10 carinae; segments II–IV with 8 carinae; segment V with 5 carinae. Telson weakly granular, almost smooth; vesicle with an oval shape; aculeus slender and longer than vesicle (see Table 1); subaculear tooth absent. Chelicerae: Not observable. Pedipalps very slender and long (see Table 1); carinae poorly preserved; femur probably pentacarinate; patella and chela almost acarinate and smooth; two dorsal vestigial carinae on the patella and one on the hand of the chela. Trichobothrial pattern very incomplete, recalling a possible 'basic' type A. Chela manus with trichobothria, **Eb_3, Eb_2, Esb** and **Et**? Fixed finger with trichobothria **eb, db** and **dt**. Patella with **d_1, d_2, d_3** and **d_5**. Femur with **d_1, d_2** or **d_3** and **e_1** and

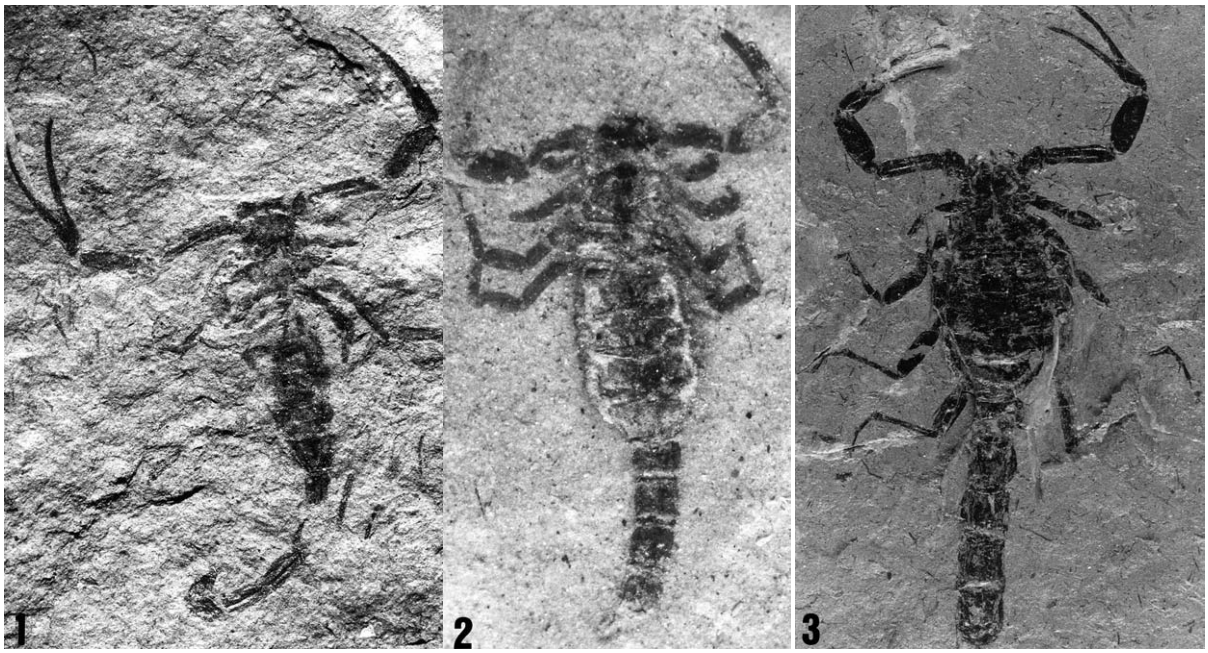

Fig. 1–3. *Protobuthus elegans* gen. n., sp. n. **1**. Holotype, possibly a male adult or pre-adult. **2**. Juvenile, paratype. **3**. *Gallioscorpio voltzi* gen. n., sp. n., holotype, dorsal aspect.

Figs. 1–3.*Protobuthus elegans* gen. n., sp. n. **1**. Holotype, probablement un mâle adulte ou pré-adulte. **2**. Juvénile, paratype. **3**. *Gallioscorpio voltzi* gen. n., sp. n., holotype, vue dorsale.

e_2? Dentate margins of fixed finger probably composed of a single linear row of granules. Legs: ventral aspect of tarsi and spurs not observable.

Superfamily Mesophonoidea Wills, 1910

Gallioscorpionidae new family

This fossil family is placed in the superfamily Mesophonoidea Wills. This decision is based mainly on the morphology of the carapace which has the median ocular tubercle placed at the anterior edge, on a prominent anterior median process. Further evidence will, however, be necessary to clarify the taxonomic position of all the elements placed in this superfamily.

Careful analysis of several characters led us to conclude that the new family described here shows some affinities with modern families, in particular the Buthidae, mainly on the basis of the position of some of the trichobothria.

Diagnosis. Scorpions of medium size (50 to 60 mm in total length). Slender body and moderately slender appendages. Carapace always wider than long; entire median ocular tubercle on the anterior edge of the carapace, situated in a protrusion or prominent anterior median process; eyes large and separated by less than one ocular diameter. Lateral eyes, apparently on an elevated protruding zone and composed of several oceles, but not compound. Sternum with a pentagonal shape, about three times longer than wide. Spiracles very small and slit-like to oval in shape. Pectines large with 31 to 38 teeth; fulcra present. Trichobothrial pattern very incomplete but recalling the 'basic' type A [20]. The following trichobothria can be observed: 2 dorso-external on chela manus; 2 on the fixed finger; 3 dorsal and 1 internal on patella; 2 dorsal, 1 external and 1 internal on the femur. Dentate margins of fixed finger probably composed of a single linear row of granules. Legs: pedal spurs present on legs III–IV. Tibial spurs present on leg IV, strong.

Type of the new family: genus ***Gallioscorpio*** new genus.

Type species: Gallioscorpio voltzi sp. n.

Diagnosis: the same as for the new family.

Gallioscorpio voltzi sp. n. (Figs. 3–9, 13–24).

Type material. Holotype; 7890 (A), France, Vosges, Voltzia Sandstone Formation, Bust (Collection Grauvogel & Gall), sex unknown in part only. Paratypes composed of a few almost complete specimens and several hundred fragments, all from France, Vosges, Voltzia Sandstone Formation. Depositary: 'Laboratoire de Paléontologie, université Louis-Pasteur', Strasbourg, France.

Etymology. The specific name is dedicated to Philippe Louis Voltz, an outstanding Alsatian geologist from the 19th century.

Coloration. In some of the best-preserved specimens, a dark reddish to almost blackish coloration can be observed, but it is uncertain whether this is original or an artefact of fossilization.

Morphology.

- Prosoma: carapace always wider than long; entire median ocular tubercle on the anterior edge of the carapace, situated on a protrusion or prominent anterior median process; eyes large and separated by less than one ocular diameter. Lateral eyes, apparently on an elevated protruding zone and composed of several oceles, but not compound. Two furrows present just behind the prominent anterior median process; a central median furrow can be observed on the posterior region of the carapace. Tegument smooth. Sternum with a pentagonal shape, about three times longer than wide.
- Mesosoma: Tergites I–VI with a median weak carina, and two transverse carinae. Tergite VII pentacarinate, with lateral pairs of carinae weak. Intercarinal spaces weakly granular, almost smooth. Sternites I-VI with vestigial carinae; no furrows are observable; VII with four weak carinae. Spiracles very small and slit-like to oval in shape. Pectines long; pectinal tooth count 31 to 38 in different specimens, possibly males and females; fulcra present. Metasoma: Segments I–IV with dorsal, ventro-lateral and ventral carinae; segment V with dorsal, ventro-lateral and some random granulations in the ventromedian area. Telson with a globular shape, weakly granular, almost smooth. Aculeus very long; subaculear tooth absent. Chelicera, with a general pattern of dentition, but closer to the Buthidae type [22]; medial and basal teeth of fixed finger spinoid; basal teeth absent from movable finger, whereas medial is stronger than subdistal. Pedipalps elongated but less than in *Protobuthus elegans*; carinae poorly preserved; femur probably pentacarinate; patella and chela almost acarinate and smooth. Trichobothrial pattern very incomplete, recalling a possible 'basic' type A. Chela manus with trichobothria, **Est** and **Esb**? Fixed fin-

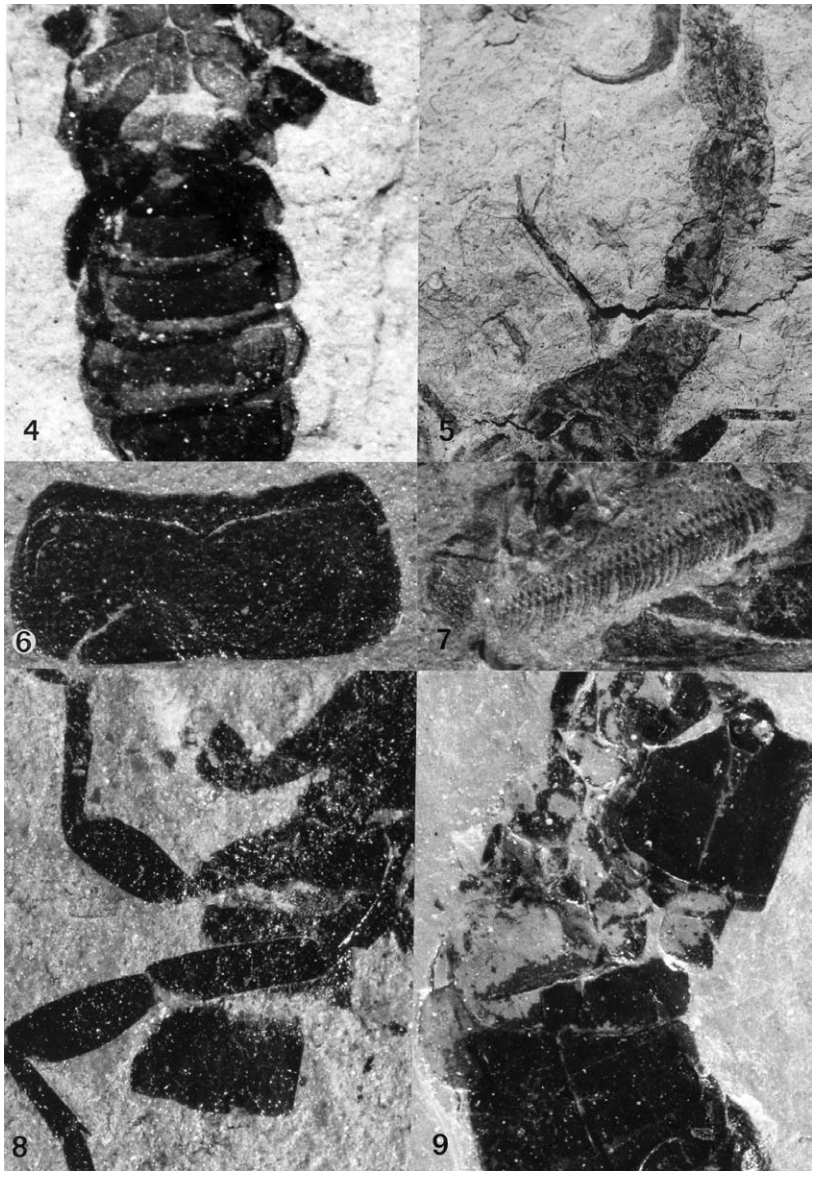

Fig. 4–9. *Gallioscorpio voltzi* gen. n., sp. n. **4–7**. Paratypes. **4**. Juvenile, ventral aspect, showing coxapophysis, sternum and sternites. **5**. Metasoma and telson, lateral aspect. **6**. Sternite V or VI. **7**. Pecten. **8**. Legs III and IV, showing pedal and tibial spurs. **9**. Carapace.
Figs. 4–9.*Gallioscorpio voltzi* gen. n., sp. n. 4–7. Paratypes. **4**. Juvénile, vue ventrale avec coxapophyse, sternum et sternites. **5**. Metasoma et telson, vue latérale. **6**. Sternite V ou VI. **7**. Peigne. **8**. Pattes III et IV avec les éperons basitarsal et tibial. **9**. Carapace.

ger with trichobothria **esb** and **est**? Patella with $\mathbf{d_1}$, $\mathbf{d_2}$, $\mathbf{d_3}$ and **i**. Femur with $\mathbf{d_1}$, or $\mathbf{d_3}$, $\mathbf{d_5}$ and $\mathbf{e_1}$. Dentate margins of fixed finger probably composed of a single linear row of granules. Legs: pedal spurs present on legs III–IV. Tibial spurs present on leg IV, strong. Ventral aspect of tarsi not observable.

4. Mode of life

The earliest scorpions occur in the Silurian and are contemporaneous with terrestrialization, i.e. the transition of animals from the aquatic habitat to land. They lived in the water and respired through gills. Terrestrial

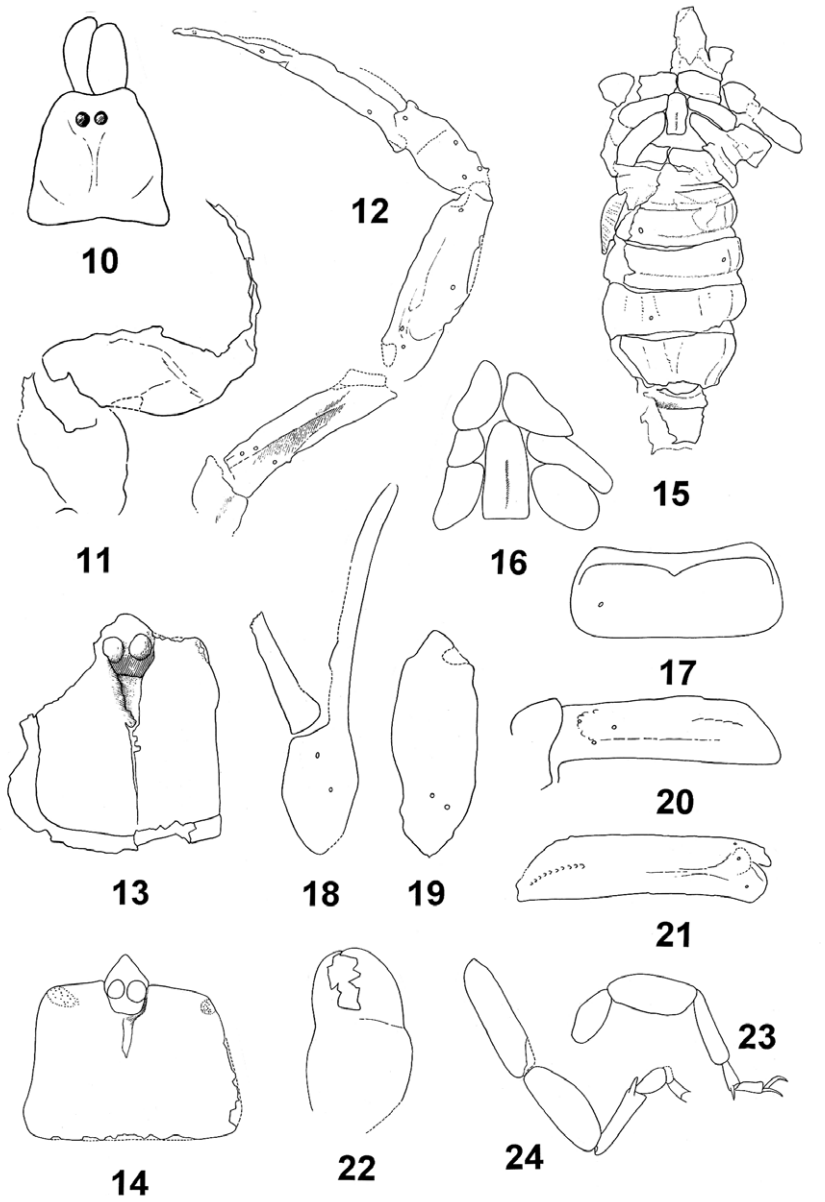

Fig. 10–24. **10–12**. *Protobuthus elegans* gen. n., sp. n. **10**. Paratype. Carapace, showing median eyes. **11–12**. Holotype. **11**. Telson, lateral aspect. **12**. Femur, patella and chela, dorsal aspect, showing trichobothria. **13–24**. *Gallioscorpio voltzi* gen. n., sp. n., paratypes. **13–14**. Carapaces, showing median and lateral eyes (cf. Fig. 9). **15**. Ventral aspect (cf. Fig. 4). **16**. Sternum in detail. **17**. Sternite (cf. Fig. 6). **18**. Chela, dorso-external aspect. **19**. Patella, dorsal aspect. **20**. Right femur, dorsal aspect. **21**. Left femur, dorso-external aspect. **22**. Chelicera. **23–24**. Legs III and IV (cf. Fig. 8.).

Figs. 10–24. 10–12. *Protobuthus elegans* gen. n., sp. n. **10**. Paratype. Carapace, avec les yeux médians. **11–12**. Holotype. **11**. Telson, vue latérale. **12**. Fémur, tibia et pince, vue dorsale, avec des trichobothria. **13–24**. *Gallioscorpio voltzi* gen. n., sp. n. Paratypes. **13–14**. Carapaces avec les yeux médians et latéraux (cf. Fig. 9). **15**. Vue ventrale (cf. Fig. 4). **16**. Sternum en détail. **17**. Sternite (cf. Fig. 6). **18**. Pince, vue dorso-externe. **19**. Tibia, vue dorsale. **20**. Fémur droit, vue dorsale. **21**. Fémur gauche, vue dorso-externe. **22**. Chélicère. **23–24**. Pattes III and IV (cf. Fig. 8.).

scorpions appear in the Carboniferous. Their respiratory organs are book lungs, opening to the outside through stigma. Aquatic genera survived until Triassic. Today, all living scorpions are terrestrial and have nocturnal activity. The Grès à Voltzia specimens undoubtedly belong to animals that lived on land. Scorpions are predators hunting on smaller animals. In the Buntsandstein landscapes, they found a large range of prey, particularly insects, at their disposal. A certain eclecticism in the choice of prey may explain the coexistence of two species, a slender beside a stockier one, in the same biotopes. Possibly, some scorpions also ate myriapods [11].

5. The Triassic recovery

The Grès à Voltzia faunas and floras are of Anisian age and belong to an interval of time corresponding with the first million of years of the Mesozoic [2]. They give evidence for the recovery of the biosphere that followed the dramatic end-Permian mass extinction. The Palaeozoic faunal reduction affected taxonomic groups differently. The Trilobites had definitely disappeared by the end of the Permian, but Early Triassic Crustacea contain genera inherited from the Palaeozoic *(Euthycarcinus, Halicyne)* that persist alongside taxa announcing the arrival of modern faunas (isopods, decapods). During the Triassic, the earliest known flies (Diptera) [16] and the oldest known mygalomorph spiders [18] appear in company of 'living fossils', i.e. taxa with very low rates of speciation, such as lingulids, coelacanths, scorpions, cockroaches (Blattodea) and the species *Triops cancriformis*, which is apparently very close to recent representatives. Such an evolutionary stasis cannot fail to intrigue. The Grès à Voltzia deltaic environment, a transitional area located between land and the aquatic realm, developed many fragmented habitats that constituted not only refuges for ancestral taxa but also cradles for the emergence of new groups.

6. Conclusion

The frequent occurrence of scorpions in the fossiliferous localities of the Buntsandstein confirms the outstanding position occupied by these arthropods among the small predators of the Triassic period. Considered as 'living fossils' or panchronological animals, the Grès à Voltzia taxa differ nevertheless both from the former Palaeozoic families and from the Mesophonidae of the Middle Triassic of Great Britain. Most remarkable is the fact that at least one family, Protobuthidae, can, to some extent, be classified together with the Cretaceous fossil family, Archaeobuthidae and the extant family Buthidae within the Superfamily Buthoidea. Modern Buthidae are therefore presumably associated with lineages at least 240 Myr old. This is considerably older than the 125-Myr age previously established for the Archaeobuthidae [13]. On the other hand, *Gallioscorpio voltzi*, which still exhibits features inherited from Palaeozoic scorpions, is related to a group of organisms that became extinct during the Triassic.

Once again, Buntsandstein appears to be a post-extinction recovery time of the biosphere when Palaeozoic survivors coexisted in particular habitats with more modern groups, before being finally supplanted by them.

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