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New and poorly known grylloblattids (Insecta: Grylloblattida) from the Lopingian of the Lebombo Basin, South Africa

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ABSTRACT

A new genus and species of the grylloblattid family Chaulioditidae, *Iphikozulu kwayayaensis* Aristov & Mostovski, gen. et sp. n., is described from the Lopingian locality of KwaYaya in KwaZulu-Natal, South Africa. This is the first record of the Chaulioditidae in Gondwanan deposits. The genera *Triadosialis* Handlirsch, 1906, *Protomia* Aristov, 2004 and *Miralioma* Aristov, 2004 are transferred to the family Chaulioditidae, and the genus *Kargalella* Martynov, 1937 is transferred to the Liomopteridae. *Neoliomopterum picturatum* Riek, 1976 from the Lopingian locality at Emakwezini Railway Station in KwaZulu-Natal is redescribed and transferred from Grylloblattida *incertae sedis* to the family Liomopteridae. The subfamily Kargalellinae Aristov, 2004 is synonymised under Liomopteridae Sellards, 1909.

KEY WORDS: Insecta, Grylloblattida, Chaulioditidae, Liomopteridae, Permian, Lopingian, Gondwana, new taxa, new synonymy.

INTRODUCTION

Grylloblattids have been found at a number of Lopingian (Upper Permian) localities in the north-eastern and eastern parts of the main Karoo Basin and in the Lebombo Basin (van Dijk 1997; Van Dijk & Geertsema 1999; Geertsema *et al*. 2002). A single representative of Megakhosaridae, *Miolopterina tenuipennis* Riek, 1976, is known from the Bulwer locality (Beaufort Group, Normandien Formation; previously known as the Estcourt Formation). The Emakwezini Railway Station locality near Empangeni (Beaufort Group, Emakwezini Formation; Normandien Formation equivalent) has yielded *Neoliomopterum picturatum* Riek, 1976. Two liomopterids, *Mioloptera stuckenbergi* Riek, 1973 and *Mioloptoides andrei* Riek, 1976, have been recorded from the Lidgetton locality (Beaufort Group, Normandien Formation) (van Dijk 1997). A nymph of uncertain affinity *Thaumatophora pronotalis* Riek, 1976, has been described from Haakdoornfontein (Ecca Group, Hammanskraal Formation; Vryheid Formation equivalent) (Riek 1976*a*). An incomplete grylloblattid forewing has been found recently at a locality near Colenso (Prevec *et al.* 2009). The Mooi River locality (Beaufort Group, Normandien Formation) has yielded the richest insect fauna, including representatives of four species in four genera, *Mioloptoides andrei* Riek, 1976, *Mioloptera stuckenbergi* Riek, 1973 (Liomopteridae), *Miolopterina tenuipennis* Riek, 1976 (Megakhosaridae) and *Liomoptoides similis* Riek, 1973 (Grylloblattida *incertae sedis*) (van Dijk 1997). The Mooi River locality is also remarkable for the high proportion of grylloblattids that have been collected. Grylloblattida represent 35 % of the insect fauna, whereas in Russian and Middle Asian localities they comprise 5–7 % of all insect remains.

Thus, the grylloblattid fauna of the South African Lopingian is represented by two families: the dominant Liomopteridae (63 % of all grylloblattids) and the considerably

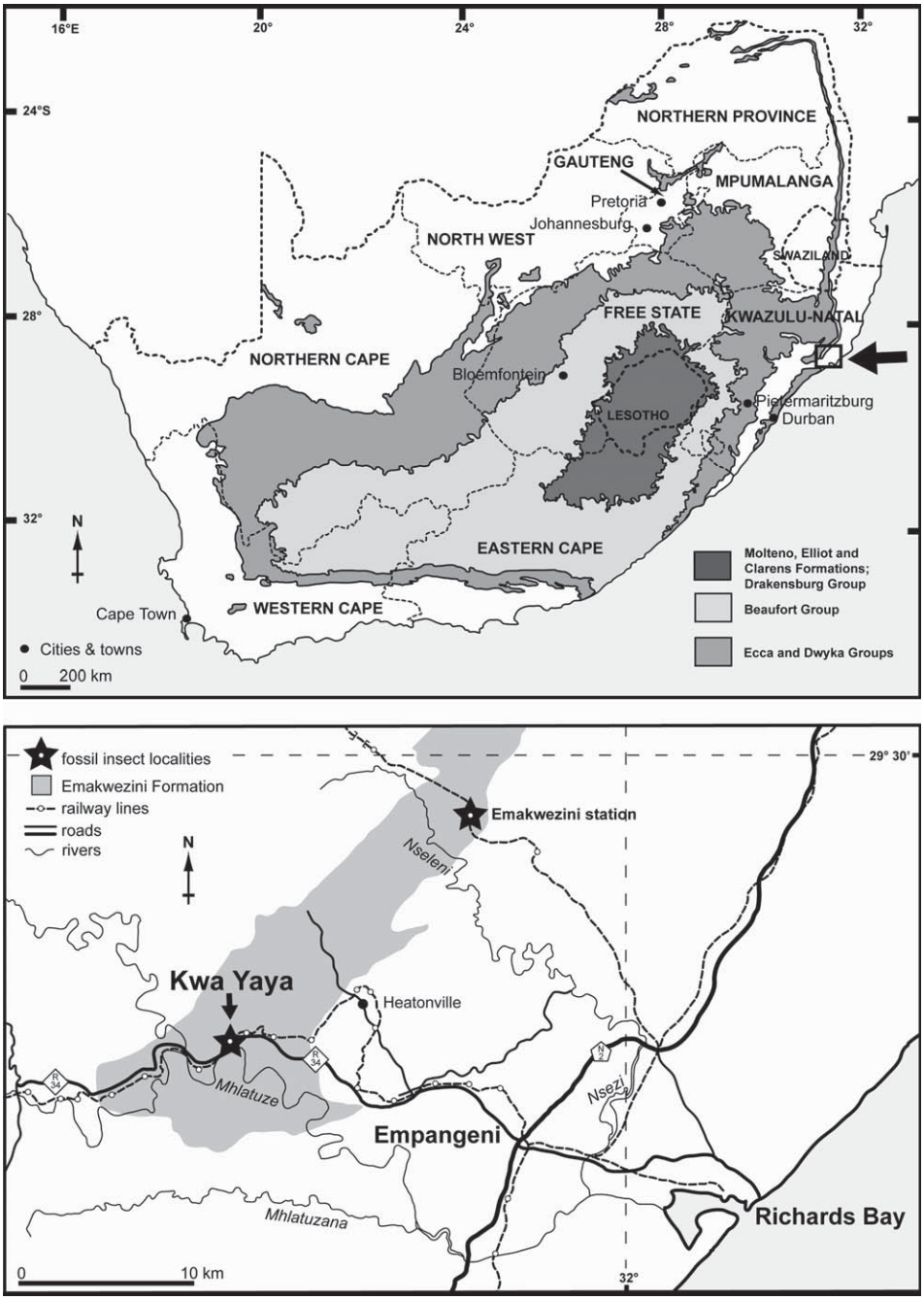

Fig. 1. Distribution of Permian and Triassic beds in South Africa and the position of two fossiliferous sites in the Lebombo Basin, KwaZulu-Natal.

rarer Megakhosaridae (22 %). The family Chaulioditidae, being widely distributed in the Tatarian (= Lopingian, or Upper Permian) of Russia, has so far been unknown in Gondwanan deposits.

A new representative of the Chaulioditidae, *Iphikozulu kwayayaensis* gen. et sp. n., is herewith described from the locality of KwaYaya in KwaZulu-Natal. In addition, *Neoliomopterum picturatum* from the contemporaneous Emakwezini Railway Station locality is transferred from Grylloblattida *incertae sedis* to the family Liomopteridae.

To summarise, the composition of the South African grylloblattid fauna is typically Lopingian, with dominating Liomopteridae, and rare Megakhosaridae and Chaulioditidae. The only difference is a high ratio (35 %) of grylloblattids to other insect taxa.

MATERIAL AND METHODS

Locality information

The holotype of *Iphikozulu kwayayaensis* gen. et sp. n. was found in fine-grained, olive-grey mudstone in a railway cutting approx. 25 km west of Empangeni along the R34 and approx. 200 m west of the KwaYaya railway siding (28°41.915'S:31°40.730'E) (Fig. 1). The holotype is housed at the Natal Museum (NMSA).

Geological setting and palaeoenvironment

The fossiliferous deposits at KwaYaya lie within the upper part of the Emakwezini Formation, Adelaide Subgroup, Beaufort Group, Karoo Supergroup. The Emakwezini Formation was deposited in the Lebombo Basin, and crops out in a narrow strip just inland of, and parallel to, the north-eastern KwaZulu-Natal coastline. The formation is considered to be lithostratigraphically equivalent to the Normandien Formation (incorporating the previously recognised Estcourt Formation) in the north-eastern and eastern parts of the main Karoo Basin (e.g., Johnson *et al.* 2006). A review of the Emakwezini Formation is provided elsewhere (Bordy & Prevec 2008).

Bordy and Prevec (2008) interpreted the autochthonous nature of the deposits at KwaYaya, together with various associated sedimentary features, as indicative of deposition in a floodplain setting in the immediate vicinity of a broad, shallow, gently meandering channel in the overbank area of a large fluvial system. According to general climatic reconstructions (Chumakov & Zharkov 2003), this locality was situated within the southern temperate semiarid belt of middle latitudes. Locally, the Emakwezini Formation appears to have been deposited under cool, humid, perennially moist conditions. The latter assumption is supported by records of grylloblattids, which are known to be associated with cold and moist environments from their early days until the present (e.g., Shcherbakov 2008) contrary to the statement that they are indicative of warmer and drier conditions (Geertsema *et al*. 2002).

Associated flora

The KwaYaya locality has yielded a glossopterid-dominated palaeoflora, containing multiple elements typical of Late Permian floras from the main Karoo Basin of South Africa (e.g., Lacey *et al.* 1975; Anderson & Anderson 1985). These include at least five morphotypes of *Glossopteris* leaves and the glossopterid ovuliferous organs *Lidgettonia africana*, *Rigbya arberioides* and *Plumsteadia gibbosa,* and the glossopterid polleniferous organ *Eretmonia natalensis*. Also present are the sphenopsids *Trizygia speciosa*, *Phyllotheca australis* and *Benlightfootia* sp. (Bordy & Prevec 2008).

TAXONOMY

Order Grylloblattida Walker, 1914

Suborder Grylloblattina Walker, 1914

Family Chaulioditidae Handlirsch, 1906

Type genus: *Chauliodites* Heer, 1864 with 11 species from the Severodvinian–Olenekian of Russia, Induan of Mongolia, Olenekian of Germany, Anisian of France and Middle Triassic of China (Aristov, 2003, 2004*b*, 2008).

Diagnosis: Costal space broader than subcostal one; M not fused with CuA, branching beyond RS base; CuA divided into CuA_1 and CuA_2.

Description: Small and middle-sized insects. Anterior margin of forewing convex. Costal space broader than subcostal one. SC ends beyond midlength or in distal third of wing. RS starts in basal third of wing, with 2–4 branches. Base of M free, M_5 absent, M bifurcates into MA and MP beyond RS base. MA with 2–4 branches, sometimes forming regular comb; MP with 1 or 2 branches. CuA bifurcates into simple CuA_1 and CuA_2, and may change its state from concave to convex almost immediately after branching. Intercubital space narrow, traversed by simple crossveins. Anal area short and broad. A_1 simple, A_2 branched. Crossveins simple, straight, forming two rows of cells in the middle of radial field. In hindwing, base of M free, M with 4 branches, CuA with 2 branches, anal area large.

Genera included: Type genus, *Triadosialis* Handlirsch, 1906 with one species from the Olenekian of Germany; *Nivopteria* Lin, 1978 with one species from the Middle Triassic of China; *Paratomia* Aristov, 2004 with one species from the Induan of Russia; *Protomia* Aristov, 2004 with one species from the Kazanian of Russia; *Miralioma* Aristov, 2004 with two species from the Kazanian and Urzhumian of Russia; and monotypic *Iphikozulu* gen. n. from the Lopingian of KwaZulu-Natal, South Africa.

Remarks: The new genus described below is characterised by the combination of a broad costal space, M branching beyond the RS base and branched CuA_1. A similar venation pattern is characteristic of the genera *Triadosialis* Handlirsch, 1906, *Protomia* Aristov, 2004 and *Miralioma* Aristov, 2004. The genus *Triadosialis* was described by Handlirsch (1906) for *Chauliodites zinkeni* Heer, 1864 from the Lower Triassic (Middle Bundsandstein) locality of Gödevitz in Germany (Heer 1864). Handlirsch assigned this genus to the family Chaulioditidae in the order Megaloptera. The family Chaulioditidae, with the only species *Ch. picteti* Heer, 1864, was transferred to the order Grylloblattida and considered a senior synonym of the family Tomiidae Martynov, 1936 (Aristov 2004*b*). The genera *Protomia* and *Miralioma* were described in the family Liomopteridae (Aristov 2004*c*). Both of them differ from other liomopterids in the M that branches late, and from chaulioditids in the branched CuA_1. The position of the M in relation to the RS base is a more reliable character than the number of CuA_1 branches. Thus, the genera *Triadosialis*, *Protomia*, *Miralioma* and *Iphikozulu* gen. n. are herewith transferred to the family Chaulioditidae, the type genus of which is characterised by the M that branches beyond the RS base. The description of the new genus and the transfer of the genera *Triadosialis*, *Protomia* and *Miralioma* to Chaulioditidae have necessitated changes to the familial diagnosis. Previously, one of the diagnostic features was simple CuA_1. Currently, a broad costal space and M branching beyond the RS base remain diagnostic for chaulioditids.

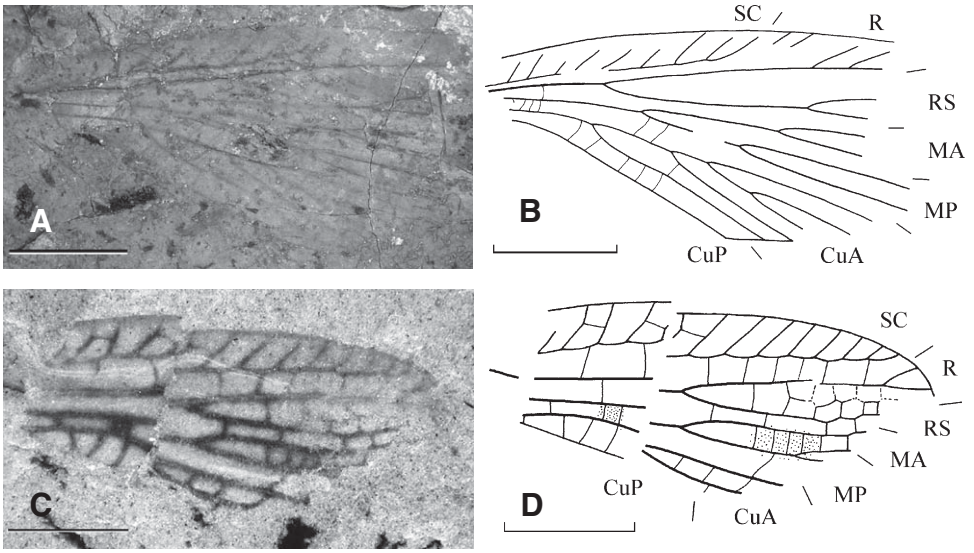

Fig. 2. New and poorly known grylloblattids: (A, B) *Iphikozulu kwayayaensis* Aristov & Mostovski, gen. et sp. n., holotype, forewing impression (A) and details of its venation (B); (C, D) *Neoliomopterum picturatum* Riek, 1976, holotype NMSA 910, forewing impression (C) and details of its venation (D). Scale bars 5 mm in Figs 2A, 2B, and 2 mm in Figs 2C, 2D.

The genus *Kargalella* Martynov, 1937 from the Urzhumian of Russia was placed in a separate subfamily of Chaulioditidae on the basis of a broad costal space and simple CuA_1. The M in *Kargalella* bifurcates proximal to the RS base (Aristov 2004*b*). The combination of these characters precludes us from keeping this genus in Chaulioditidae, and it is transferred to the family Liomopteridae, with the subfamily Kargalellinae Aristov, 2004 being considered as a new junior subjective synonym of Liomopteridae Sellards, 1909. *Kargalella* differs from other liomopterids in the combination of fused RS+MA and simple CuA_1.

An incomplete grylloblattid forewing, which has been recently found at a locality near Colenso (Prevec *et al.* 2009: 486, pl. XIV, figs 1, 2), also probably belongs to Chaulioditidae on the grounds of its wing venation. Regrettably, its further identification is difficult without a closer examination of the specimen.

Genus **Iphikozulu** Aristov & Mostovski, gen. n.

Etymology: From Zulu *iPhiko* (wing) and *Zulu* (Zulu Kingdom). Gender masculine.

Type and only species: *I. kwayayaensis* Aristov & Mostovski, sp. n.

Diagnosis: Middle-sized insects. Costal space near RS base 3 times as broad as subcostal one. SC with simple anterior branches, ends before distal third of wing. RS starts in basal quarter of wing. CuA_1 starts branching before midlength, with four branches.

Comparison: The new genus is closest to *Protomia* from the Kazanian deposits of Russia, from which it differs in simple branches of SC, as well as in CuA_2 and CuP ending on the posterior margin of the wing. In *Protomia*, CuA_2 anastomoses with CuA_1, and CuP terminates on CuA_2 (Aristov 2004*c*).

Iphikozulu kwayayaensis Aristov & Mostovski, sp. n.

Figs 2A, 2B

Etymology: From the type locality, KwaYaya.

Description: Forewing impression approx. 18 mm long, approx. 9 mm wide. Anterior margin of wing convex. RS starts branching in distal third of wing, with 2 or more branches. MA and MP with 2 branches each, start branching proximal to RS fork. CuP bent basally, straight afterwards. Crossveins simple.

Holotype: NMSA 2736 (field no. KY785a, b), the part and counterpart of a single insect wing impression. SOUTH AFRICA: *KwaZulu-Natal*: KwaYaya locality (see detail information under Material and Methods); Permian, Lopingian, Beaufort Group, Emakwezini Formation.

Family Liomopteridae Sellards, 1909

Genus *Neoliomopterum* Riek, 1976

Type and only species: *N. picturatum* Riek, 1976, by monotypy.

Diagnosis: Small insects. Anterior margin of forewing weakly convex, costal space slightly broader than subcostal one. SC with simple anterior branches, enters C near wing tip. RS base near wing midlength, at level of separation of M into MA and MP. Branches of CuA simple.

Neoliomopterum picturatum Riek, 1976

Figs 2C, 2D

Neoliomopterum picturatum: Riek 1976*b*: 763, pl. 1, fig. 7; Carpenter 1992: 111; Storozhenko 1998: 188.

Redescription: Forewing length approx. 7 mm, width approx. 3.5 mm. R with one simple anterior branch. Stems of RS, MA and MP thickened basally and near wing midlength, abruptly thinning out in distal quarter, RS and MA simple, MP with 2 branches. Branches of CuA thickened. Crossveins simple and forming double row of cell in inter-radial field. Colour pattern in form of spots in intermedial and medial fields.

Holotype: NMSA 910 (Type no. 1972), impression of well-preserved brachypterous forewing without anal field. SOUTH AFRICA: *KwaZulu-Natal*: Emakwezini Railway Station nr Empangeni; Permian, Lopingian, Beaufort Group, Emakwezini Formation.

Remarks: *N. picturatum* had originally been described as a forewing fragment of a representative of the family Liomopteridae (Riek 1976*b*). It remained in this family until some time ago (Carpenter 1992), but later was transferred to Grylloblattida *incertae sedis* on the basis of its incomplete preservation (Storozhenko 1998). Re-examination of the holotype illustrated by a photograph in the original description has shown that the preservation of the wing is almost complete. This species is characterized by a shortened wing, which is twice as long as it is broad (wings of the majority of grylloblattids are three times as long as broad), and by the stems of RS, MA, MP and CuA thickened basally and at the wing midlength. Such characters are typical of shortened wings, which can be divided into brachypterous and micropterous forms. In brachypterous individuals, the wing is longer than half of a fully developed wing, and does not have considerably modified venation. In micropterous individuals, the wing is shorter than half of a normal wing, and both its shape and venation are heavily modified (Sinitshenkova 1987). Shortened wings are recorded in some grylloblattids. Micropterous wings are known in *Protoblattiniella minutissima* Meinier, 1912 from the Upper Carbo-

niferous locality of Commentry in France and *Sylvamicropteron harpax* Aristov, 2004 from the Kungurian locality of Tshekarda in Russia. The genus *Protoblattiniella* belongs to the family Protoperlidae (Storozhenko 2002), and *Sylvamicropteron* has been described as Grylloblattida *incertae sedis* (Aristov 2004*a*). Despite the unusual proportions of the wing, *N. picturatum* still displays venation typical of grylloblattids, suggesting that we are dealing with a brachypterous wing. A rather wide costal space that is traversed by simple branches of SC, and a simple CuA_1 are features typical of two grylloblattid families, viz. Liomopteridae and Chaulioditidae. The latter family is characterized by M being divided into MA and MP beyond the RS stem (Aristov 2004*b*). This character is missing in *Neoliomopterum*, which favours its assignment to the Liomopteridae. *N. picturatum* differs from other liomopterids in having both a long SC, which reaches the wing apex, and oligomerized venation of RS, MA, MP and CuA_1. These differences are possibly caused by changed proportions of the wing, but the comparison with other known liomopterids does not offer an opportunity to synonymise this genus.

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